FOSSIL MAMMALS OF AFRICA No. 18: EAST AFRICAN MIOCENE AND PLEISTOCENE CHALICOTHERES

BY

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SYNOPSIS

The European and Asiatic species of *Chalicotherium* (*C. goldfussi*, *C. grande*, *C. grande rhodanicum*, *C. styriacum*, *Chalicotherium* sp., *C. wetzleri*, *C. salinum*, *C. brevirostris* and *C. pilgrimi*) are reviewed. A new species, *Chalicotherium rusingense* from the Lower Miocene of Kavirondo Gulf area, Kenya is described and figured in detail.

Pleistocene material from Olduvai Gorge, Tanganyika is identified with *Ancylotherium hennigi* (Dietrich) and its relationship with the Lower Pliocene species *A. pentelicum* (Gaudry & Lartet) from Greece and Iran is confirmed.

Ancylotherium and the related genera *Phyllotillon* and (*Metaschizotherium*) are discussed and *Phyllotillon betpakdalensis* (Flerov) is made the type species of a new genus *Borissiakia*.

INTRODUCTION

Chalicotheres are known to have inhabited Eurasia from the Upper Eocene (*Eomoropus*) to the Pleistocene (*Nestoritherium*), but in Africa only Pleistocene forms have hitherto been described (Andrews 1923, Hopwood 1926, Dietrich 1942, George 1950). Additional material from the Pleistocene of Olduvai Gorge, Tanganyika, is described in this paper ; it is identified as *Ancylotherium hennigi* (Dietrich) and its relationship to *A. pentelicum* from the Lower Pliocene of Greece and Iran is confirmed.

Much more abundant material has been obtained from Rusinga, Koru and other supposedly Lower Miocene sites in the Kavirondo Gulf area of Kenya. This material represents a new species, *Chalicotherium rusingense*, a primitive relation of the well-known *C.* (=*Macrotherium*) *grande* of the Upper Miocene of Europe. The same species occurs at Napak, Uganda (Butler 1962).

The main centre of chalicotherian evolution appears to have been in Asia. By Oligocene times two main branches of the family had differentiated : the Schizotheriinae and the Chalicotheriinae. Though members of both branches invaded Africa, this continent seems to have formed an evolutionary backwater, for both the known African genera occurred in Europe at earlier dates : *Chalicotherium* in the Upper Oligocene and *Ancylotherium* in the Lower Pliocene.

Most of the material described is the property of the National Museum of Kenya, Nairobi, and I wish to express my best thanks to Dr. L. S. B. Leakey for permission to study it. Acknowledgement is also due to Dr. E. I. White, F.R.S., for access to African chalicotherian material in the British Museum (Natural History), and to Dr. W. W. Bishop for the loan of specimens that he collected at Napak. Extensive use was made for comparative purposes of the important collections of chalicotherian material in the British Museum and in the Muséum d'Histoire Naturelle in Paris, and I am greatly indebted to the staff of these museums for much valued assistance, particularly to Father R. Lavocat and to Dr. A. J. Sutcliffe. I also wish to acknowledge the kindness of Prof. J. Viret and Prof. E. Kuhn-Schneider in sending casts of specimens, and of Prof. H. Tobien and Prof. S. Schaub in giving valuable advice.

Subfamily CHALICOTHERIINAE

Genus ***CHALICOTHERIUM*** Kaup, 1833

Review of European and Asiatic Species

The type species of *Chalicotherium* is *C. goldfussi* Kaup (1833) from the Pontian of Europe, ranging from Spain through Germany to Greece. This replaces the Upper Miocene species usually known as *Macrotherium grande* (de Blainville 1849), which was based on material from Sansan (Vindobonian). There is little doubt that *M. grande* is directly ancestral to *C. goldfussi* and the late Vindobonian *M. grande rhodanicum* Depéret (1892) and the Nikolsburg (Sarmatian) material described by Abel (1922) are transitional. A generic distinction between *Macrotherium* and *Chalicotherium* is therefore not justified, and *Macrotherium* must fall into synonymy (von Koenigswald 1932). The ancestor of *C. grande* is probably *C. wetzleri* Kowalewsky (1874) from the Aquitanian. No specimens of *Chalicotherium* have been recorded from European strata of undoubted Burdigalian age.

C. salinum (Forster Cooper) from the Chinji and Nagri formations of the Siwaliks (probably late Miocene to early Pliocene, Thenius 1959) is closely related to *C. grande*. However, *C. brevirostris* (Colbert 1934) from the Upper Miocene of Mongolia is quite distinct from the European species, and may be the ancestor of the Pleistocene genus *Nestoritherium.* The only other Asiatic species, *C. pilgrimi* (Forster Cooper), is a very primitive form resembling *Schizotherium.* Von Koenigswald (1932) included *Schizotherium turgaicum* Borissiak in the genus *Chalicotherium,* but additional information on its structure (Borissiak 1946, Belyaeva 1954) has confirmed its relationship to *Schizotherium priscum. Moropus matthewi* Holland & Peterson and *M. merriami* Holland & Peterson were also transferred to *Chalicotherium* by von Koenigswald following a suggestion by Matthew (1929), but on what appear to me to be insufficient grounds.

Chalicotherium goldfussi Kaup

Text-figs. 1E, 5H, 13

1823 *Pangolin gigantesque,* Cuvier, p. 193, pl. 16, figs. 26, 27.
1832 *Manis gigantea* Cuvier ; Kaup & Scholl, p. 7.
1832 *Lophiodon Goldfussi* Kaup & Scholl, p. 10 (Nomen nudum?)
1833 *Chalicotherium goldfussi* Kaup, pp. 4–6, pl. 7, figs. 3–5.
1833 *Chalicotherium antiquum* Kaup, pp. 6, 7, pl. 7, figs. 6, 7.
1844 *Macrotherium giganteum* Pictet, p. 232, pl. 8, fig. 5.
1849 *Chalicotherium goldfussi* Kaup ; de Blainville, p. 82, pl. 8.
1849 *Chalicotherium antiquum* Kaup ; de Blainville, p. 83, pl. 8.
1859 *Chalicotherium goldfussi* Kaup ; Kaup, p. 1, pl. 1, figs. 1–3, 5.
1859 *Chalicotherium antiquum* Kaup ; Kaup, p. 1, pl. 1, figs. 4, 7.
1885 *Chalicotherium baltavarensis* Pethö, p. 69.
1886 *Chalicotherium goldfussi* Kaup ; Lydekker, p. 162 (in part).
1891 *Chalicotherium antiquum* Kaup ; Schlosser, p. 87.
1920 *Chalicotherium Goldfussi* Kaup ; Abel, p. 30, text-figs. 3, 5, 7.
1922 *Chalicotherium goldfussi* Kaup ; Abel, p. 118, text-figs. 108–111.
1927 *Chalicotherium goldfussi* Kaup ; Barnes, p. 22, text-fig. 7.
1929 *Chalicotherium* cf. *goldfussi* Kaup ; Arambourg & Piveteau, p. 23, pl. 3, figs. 1–3.
1929 *Chalicotherium goldfussi* Kaup ; Matthew, p. 518.
1932 *Chalicotherium goldfussi* Kaup ; von Koenigswald, p. 14, pl. 1, figs. 9, 10 ; pl. 3, fig. 37.
1937 (?) Ancylopoda gen. et sp. indet., Bohlin, p. 104, pl. 9, figs. 7–9.
1939 *Chalicotherium goldfussi* Kaup ; Wehrli, p. 26, pls. 1, 2.
1943 *Chalicotherium goldfussi* Kaup ; Villalta & Crusafont, p. 153, text-fig. 24, pl. 9, figs. 3–5.
1949 *Chalicotherium goldfussi* Kaup ; Zapfe, p. 69, text-figs. 1–3.

The type material is Pontian, but the palate and cervical vertebra described by Abel (1922) from Nikolsburg are probably Sarmatian (Thenius 1959). A metacarpal II (M.11349) and an astragalus (M.11351) (Text-fig. 13) from Pikermi, now in the British Museum (Natural History), belong to *Chalicotherium* and may be referred to this species. A phalanx from Tsaidam, China, described by Bohlin (1937) may also belong to this species.

Wehrli (1939) has redescribed the teeth and phalanges from the type locality (Eppelsheim). The molars are larger and proportionately broader than in the type material of *C. grande* from Sansan, but are not so clearly distinguishable from *C. grande rhodanicum.* The protocone is usually isolated from the protoconule (Matthew 1929), the Nikolsburg specimen being intermediate in this respect. The premolars are more reduced, and P_2 is absent in a specimen from Salonica

(Arambourg & Piveteau 1929). P_2–P_4 are figured by Barnes (1927) ; the two associated teeth identified by Wehrli (1939) as P_3 and P_4 are probably P_4 and M_1 respectively. In the juvenile skull from Salonica the unerupted P^3 and P^4 show a partial division of the deuterocone into protocone and hypocone, as in some specimens of *Moropus* (Osborn 1890).

C. baltavarensis is based on a mandibular fragment containing a molariform tooth. A cast of this specimen is in the British Museum (Natural History). The tooth is fully molariform and therefore unlikely to be a premolar. It is too small (length 25 mm.) for a molar of *C. goldfussi*. The lack of a metastylid excludes *Ancylotherium pentelicum*, to which Schlosser (1891) referred it. It is tentatively identified as Pd_4 of *C. goldfussi*. Anteriorly there are alveoli for Pd_3 and Pd_2, and then a short diastema (20–25 mm.). According to Pethö (1885), there is a trace of a canine alveolus at the anterior end of the specimen.

The metacarpal from Pikermi is very much like specimens of *C. grande*. The astragalus from Pikermi is relatively lower than in *C. grande*, and has a more extensive contact with the cuboid. Metatarsal III (Zapfe 1949) is broader than in *C. grande*. Basal phalanges described by Wehrli (1939) and by Villalta & Crusafont (1943) are larger than in typical *C. grande*. Wehrli's fig. 26 shows a phalanx from the manus and fig. 25 one from the pes ; in the manus the metacarpal facet occupies a greater proportion of the dorsal surface than in *C. grande*.

Macrotherium giganteum Pictet was based upon a combination of the ungual phalanx from Eppelsheim described by Cuvier (=*C. goldfussi*) and Lartet's material from Sansan (=*C. grande*). The specific name *giganteum* has priority over *grande*, and in order to avoid changing a well known name I here select the ungual phalanx as the lectotype of Pictet's species, which thus becomes synonymous with *C. goldfussi*.

Chalicotherium grande (de Blainville)

Text-figs. 1D, 4C, D, 5G, 8C, 10G–L, 11F–J, 12F–J, 13–15, 16E, 17D

1837 *Anoplotherium* Lartet, p. 88.
1837*a* *Macrotherium* Lartet, p. 424.
1839 *Anoplotherium magnum* Lartet, p. 26. Nomen nudum.
1844 *Macrotherium giganteum* Pictet, pp. 232, 233 (in part). See also discussion of *C. goldfussi* above.
1848 *Anisodon* (*Choelichotherium*) Pomel, p. 686.
1849 *Anoplotherium grande* ' Lartet ' ; de Blainville, p. 66, pls. 3, 8.
1849 *Chalicotherium anisodon* de Blainville, pp. 68, 152, pl. 9.
1850 *Chalicotherium grande* (de Blainville) Gervais, p. 91.
1850 *Macrotherium giganteum* ' Lartet ' ; Gervais, p. 135, pl. 43.
1851 *Macrotherium sansaniense* Lartet, p. 22.
1851 *Anisodon magnum* Lartet, p. 30. (The name *Anisodon* first appears in the MS catalogue of Lartet's collection (dated 1847). This is the " Cat. Man. " referred to by Lartet (1851). It is preserved in the Paris Museum).
1853 *Chalicotherium grande* ' Gervais ' ; Pictet, p. 337, pl. 15, fig. 6.
1855 *Macrotherium* Lartet ; de Blainville, p. 37, explanation of unnumbered plate.
1859 *Anisodon larteti* Kaup, pl. 2, figs. 1–5 (=*Chalicotherium antiquum*, in part).
1847 *Chalicotherium* (*Anisodon*) ; Kowalewsky, p. 175, pl. 8, figs. 73, 74.

1877 *Macrotherium giganteum* ' Lartet ' ; Gervais, p. 226, pl. 2, figs. 2–5.
1886 *Chalicotherium goldfussi* Kaup ; Lydekker, p. 161 (in part).
1891 *Chalicotherium magnum* (Lartet) Filhol, p. 294, pls. 43–46.
1892 *Macrotherium grande* ' Lartet ' ; Depéret, p. 61.
1893 *Macrotherium giganteum* 'Lartet ' ; Osborn, p. 121, text-fig. 3.
1898 *Macrotherium grande* ' Lartet ' ; Roger, p. 29, pl. 3, fig. 7.
1902 *Chalicotherium anisodon* de Blainville ; Schlosser, p. 212. (States the name has priority but rejects because of non-usage).
1913 *Macrotherium grande* ' Lartet ' ; Holland & Peterson, pp. 209, 217, text-figs. 4, 15, 98.
1913 *Macrotherium grande* ' Lartet ' ; Wegner, p. 246, pl. 14, figs. 27–30.
1920 *Macrotherium magnum* Lartet ; Abel, p. 50, text-figs. 11, 13, 14.
1922 *Macrotherium magnum* Lartet ; Abel, p. 197, text-fig. 162A, B.
1923 (?) *Macrotherium oggenhausense* Dietrich, p. 190, text-fig. 1. (See Schlosser 1926).
1925 *Macrotherium grande* ' Lartet ' ; Stehlin, p. 139, text-fig. 18*a*, *b*.
1928 *Macrotherium grande* ' Lartet ' ; Dietrich, p. 367.
1932 *Chalicotherium grande* '(Lartet)' ; von Koenigswald, pp. 10, 13, pl. 1, figs. 8, 9, 14–17 ; pl. 2, fig. 22 ; pl. 3, figs. 30–36.
1935 *Macrotherium sansaniense* Lartet ; Boule & Piveteau, p. 637, text-figs 1026, 1029.
1936 *Macrotherium magnum* Lartet ; Bohlin, p. 323.
1943 *Macrotherium grande* ' Lartet ' ; Villalta & Crusafont, p. 125, text-figs. 1–23, pls. 1–9.
1949 *Chalicotherium grande* '(Lartet)' ; Zapfe, p. 69, text-figs. 1–3.
1949*a* *Chalicotherium grande* '(Lartet)' ; Zapfe, p. 176.
1958 *Chalicotherium grande* '(Lartet)' ; Mottl, p. 46.
1964 *Chalicotherium grande* de Blainville ; Ginsberg, p. 11.

The erroneous ascription of the name *grande* to Lartet began with de Blainville (1849). In 1837 Lartet did not use a specific name but merely referred to " un grand Anoplotherium " ; in 1839 he used the name *magnum* for the same material (without description).

Chalicotherium grande is characteristic of the Vindobonian of Europe. Details of its anatomy have been described in many papers, of which the more important are as follows : de Blainville (1849) figured teeth, skull and mandible, and also (1855) limb-bones and vertebrae. Lartet (1851) described the skeletal remains from Sansan. Gervais (1850) re-figured the limb-bones and also figured an atlas vertebra. Gaudry (1862) gave various details of the limb-bones which he compared with *Ancylotherium*. Kowalewsky (1874) figured some teeth. Gervais (1877) discussed and figured the feet. Filhol (1891) gave an account of his discovery of a fairly complete skeleton including a skull, unfortunately badly crushed ; he described various details of the skull figured by de Blainville and figured some mandibles, one of them containing milk dentition. Wegner (1913) described some teeth and an astragalus. Holland & Peterson (1913) gave a new restoration of the manus, figured the astragalus, and compared the various bones in some detail with those of *Moropus*. Abel (1920) compared *C. grande* (" *Macrotherium* ") with *Ancylotherium* (" *Chalicotherium* ") ; his conclusions were criticised by Dietrich (1928). Von Koenigswald (1932) compared *C. grande* with *Metaschizotherium* and figured a molar and some phalanges. Villalta & Crusafont (1943) described teeth and limb-bones, including a number from a single individual. Zapfe (1949) figured a third metatarsal which he compared with *C. goldfussi*.

The specimen from Sansan figured by de Blainville as *C. anisodon* and by Filhol as *C. magnum* var. *secundarium* is pathological. P_2 is separated from P_3 and lies in the diastema, considerably tilted forwards in the jaw. There exists in Paris another half-mandible with normal premolar alveoli, which appears to belong to the opposite side of the same individual.

Chalicotherium grande rhodanicum (Depéret)

1887 *Chalicotherium* aff. *modicum* Depéret, p. 228, pl. 13, fig. 35.
1892 *Macrotherium grande* var. *rhodanicum* Depéret, p. 63, pl. 2, fig. 1, pls. 3, 4.

Specimens from La Grive St. Alban are larger and more progressive than typical specimens of *C. grande* from Sansan, and are distinguished as the subspecies *rhodanicum*.

C. grande rhodanicum is known from an incomplete skull and mandible, together with metacarpals and phalanges (Depéret 1892). Isolated molariform teeth compared by Depéret (1887) with *C. modicum* (=*Schizotherium priscum*) are probably milk molars of *C. grande rhodanicum*. Depéret's statement that metacarpal II has almost no contact with the trapezoid is not borne out by his figure.

Chalicotherium styriacum Bach

Text-fig. 4E

1913 *Chalicotherium styriacum* Bach, p. 688, pl. 28, fig. 1*a*, *b*.

This species is based on a mandible from Eggersdorf (probably of Pontian age), a cast of which is in the British Museum (Natural History). It is rather small, considering its late date : the molars fall into the size range of *C. grande* from Sansan. The metastylid is more distinct than in any known specimen of *C. grande*, and, so far as can be judged from the worn teeth, the entoconid of P_4 is absent.

Chalicotherium sp.

1913 *Chalicotherium* sp., Bach, p. 687, pl. 28, figs. 2–4.

Bach (1913) described some mandible fragments and an incomplete upper molar from Voitsberg, regarded as Middle Miocene by Pia & Sickenberg (1934). They appear to represent a smaller form than *C. grande*. The total length of the lower molars is 82 mm., whereas in specimens of *C. grande* from Sansan this measurement ranges from 90 to 105 mm. In an unworn molar there is a small but distinct metastylid.

Chalicotherium wetzleri Kowalewsky

Text-fig. 8B

1837 *Palaeotherium schinzii* Meyer, p. 676. (Nomen nudum).
1847 *Chalicotherium wetzleri* Kowalewsky, p. 248, pl. 8.
1883 *Chalicotherium modicum* Gaudry ; Schlosser, p. 165.

1891 *Chalicotherium wetzleri* Kowalewsky ; Schlosser, p. 87.
1914 *Chalicotherium wetzleri* Kowalewsky ; Stehlin, p. 187.
1929 *Macrotherium wetzleri* (Kowalewsky) Viret, p. 267.
1932 *Schizotherium wetzleri* (Kowalewsky) von Koenigswald, p. 16, pl. 1, fig. 7.

Palaeotherium schinzii was based on a mandible from Bollingen, now in Zürich. I am greatly indebted to Prof. Tobien for his help in finding this specimen, and to Prof. Kuhn-Schneider for sending me a cast (Text-fig. 8B). The identity of *P. schinzii* with *C. wetzleri* was suggested by Schlosser (1891) and accepted by Stehlin (1914). The name *Anisodon schinzii* mentioned by Schlosser does not appear to have been published previously, and may have been a manuscript name. The original description is very brief : " um ein Viertel kleiner als *Palaeotherium magnum* und ungefähr eben so viel grösser als *Palaeotherium crassum* ". Prof. Schaub kindly informs me that it was Stehlin's opinion that this poor characterisation could not validate the name *schinzii*, taking into account the great diversity of *Palaeotherium* species. Rather than revive a name that has been unused for well over a century it seems wise to accept this opinion.

C. wetzleri is Aquitanian in age, and might be expected to be more primitive than *C. grande*. Nevertheless the size difference is slight. The total molar length is 92 mm. on the Bollingen mandible, and slightly more in a specimen measured by von Koenigswald (1932), and the molars therefore fall within the lower part of the size range of *C. grande* from Sansan. The premolar/molar index is rather high (54), but still within the range of *C. grande* (47–55). M_3 is similar to M_2, a clear distinction from *Schizotherium*, where M_3 has an enlarged hypoconulid. The main difference from *C. grande* is the presence of a distinct metastylid, a primitive character found also in *Schizotherium*. Pd^4 and Pd^3 also resemble *Schizotherium* in the completeness of the protoloph. The Bollingen mandible differs from *C. grande* in that the step in the upper border anterior to P_2 is a little more pronounced. The diastema seems to have been at least as long as in *C. grande*, but the anterior end of the jaw is not preserved. A juvenile mandible from St. Gérand-le-Puy described by Filhol (1879) belongs not to *C. wetzleri*, as Viret (1949) suggested, but to *Phyllotillon*.

Viret (1929) referred to *C. wetzleri* two basal phalanges, one apparently from the manus, the other from the pes. They are much smaller in proportion to the teeth than in *C. grande*, and reference is somewhat doubtful. They might belong to an unknown smaller species, or to *Phyllotillon*.

Whether *Chalicotherium* was present in the Stampian is still uncertain. According to Filhol (1877), chalicotherian material from the Phosphorites of Quercy is not homogeneous, and primitive species of *Chalicotherium* might have been confused with *Schizotherium priscum*.

Chalicotherium salinum (Forster Cooper)

1876 (?) *Manis sindiensis* Lydekker, p. 64, pl. 8, figs. 11–14.
1922 *Macrotherium salinum* Forster Cooper, p. 542, text-figs. 1–3.
1929 *Macrotherium salinum* Forster Cooper, ; Matthew, p. 517.
1932 *Chalicotherium salinum* (Forster Cooper) von Koenigswald, p. 22.
1935 *Macrotherium salinum* Forster Cooper ; Colbert, p. 167, text-figs. 72–76.

This species is known from the Chinji and Nagri (late Miocene—early Pliocene) formations of the Siwaliks. It is based on an isolated M^3 ; additional material was described by Colbert (1935). It averages rather smaller than *C. grande.* In the upper molars the protoloph is complete, and there is a sharp ridge on the buccal slope of the paracone. A basal phalanx of the manus is proportionately a little narrower than in *C. grande.* In two middle phalanges there is a very prominent volar process at the proximal end, uncommon in *C. grande* but present in the phalanx that constitutes the holotype of *Manis sindiense.* In other respects *C. salinum* appears to agree closely with *C. grande,* and the two species are undoubtedly closely related.

Chalicotherium brevirostris (Colbert)

1934 *Macrotherium brevirostris* Colbert, p. 374, text-figs. 11, 12, 13*a, c, e, g* (?*d, f*), 14*i* (?*h, l*).
1934 *Macrotherium* sp., Colbert, p. 381, text-figs. 14*h, k–o.*

This species is known only from the Tung Gur formation (Upper Miocene) of Mongolia. The upper molars agree in size and proportions with those of *C. grande,* but the premolars are more reduced, as in *C. goldfussi.* In the holotype the protoloph of the molars is complete, as in *C. salinum.* The skull differs from that of *C. grande* in several respects, detailed by Colbert (1934). Upper canines are absent. The lower jaw and teeth are unknown.

The only postcranial bones known are a metatarsal IV and some phalanges. The metatarsal is rather small and may belong to a smaller individual than the skull. The width and thickness of its shaft bear the same proportion to the length of the bone as in *C. grande,* but the dorsovolar diameters of the proximal and distal ends are proportionately greater ; in lateral view the ends of the bone project beyond the dorsal surface of the shaft, whereas in *C. grande* the dorsal surface of the metatarsal is nearly flat. A basal phalanx, probably from digit II of the pes (Colbert 1934 fig. 13*c*) agrees well in size and proportions with specimens of *C. grande.* Two other basal phalanges may reasonably be referred to *C. brevirostris,* though Colbert believed that they belonged to a larger species. One (fig. 14*l*) agrees well in size with phalanges of *C. grande* from digit III of the manus, though it is rather more parallel-sided and less broadened proximally than in most specimens of that species. It is not very different, however, from a phalanx from Spain figured by Villalta & Crusafont (1943). In shape it also resembles a phalanx of *C. salinum,* which is smaller in size. A phalanx probably from digit IV of the pes (fig. 14*h*) is a little larger than in *C. grande* ; its metatarsal articulation occupies a somewhat smaller proportion of the dorsal length than in that species. Five of the six middle phalanges figured by Colbert, though differing greatly in size, can be matched with specimens of *C. grande,* and there is no reason why they should not be referred to *C. brevirostris.* The aberrant specimen (fig. 13*d*), which has a more dorsally facing proximal articulation, might belong to one of the Schizotheriinae. This may also be true of the ungual phalanges, which are much lower in proportion to their length than in *C. grande.* One of them (fig. 13*f*) is also very broad, with a wide cleft, resembling a specimen of *Schizotherium turgaicum* figured by Belyaeva (1954).

Chalicotherium pilgrimi (Forster Cooper)

Text-figs. 1B, 4A, 14

1910 *Schizotherium* sp. ind., Pilgrim, p. 67.
1912 *Schizotherium* sp. ind., Pilgrim, p. 36.
1920 *Schizotherium pilgrimi* Forster Cooper, p. 362.
1929 *Schizotherium pilgrimi* Forster Cooper ; Matthew, p. 518.
1932 *Chalicotherium pilgrimi* (Forster Cooper) von Koenigswald, p. 22.
1935 *Schizotherium pilgrimi* Forster Cooper ; Colbert, p. 162.

This species, from the Bugti Beds (Lower Miocene) of Baluchistan, resembles *Schizotherium priscum* in its relatively small size, and also in most features of the upper molar pattern, for example the relatively buccal position of the ectoloph (Text-fig. 1B). However, the length/width index of M^2 is 106, which is lower than in *S. priscum* (110–115) but falls within the range of *C. grande* (104–111). There is a well-developed metastylid on M_1 and Pd_4, present in *Schizotherium* but also in *C. wetzleri*.

Although Forster-Cooper did not refer any postcranial material to this species, he described from the same beds a metatarsal II (Text-fig. 14) and two basal phalanges which are undoubtedly chalicotheriine and probably belong to *C. pilgrimi*. The only other chalicothere so far recognised from the beds is *Phyllotillon naricus* Pilgrim, a schizotheriine which could not be the possessor of the bones in question ; moreover, phalanges referable to this species occur. If the metatarsal and phalanges are correctly referred to *C. pilgrimi*, it would be necessary to follow von Koenigswald (1932) in removing the species from *Schizotherium*, in spite of the retention of primitive characters in the teeth.

Chalicotherium rusingense sp. nov.

Text-figs. 1–20

DIAGNOSIS. A small species of *Chalicotherium* with teeth similar in size to those of *C. pilgrimi* and *Schizotherium priscum* ; resembling these in the presence of a metastylid on the lower molars (except in a few individuals), but differing from them in that the paracone and metacone are situated about half-way across the crown. Canines present in both jaws ; incisors $^0/_3$. Snout relatively elongated ; diastema proportionately longer than in *C. grande*. Astragalus less depressed than in *C. grande*. Basal phalanges of the manus more elongated than in *C. grande*, especially in digit III.

HOLOTYPE. B.M.N.H., no. M.25270. A left maxilla with upper dentition, from site R107, Rusinga Is.

DISTRIBUTION. Lower Miocene (?) beds of Kenya (Rusinga, Karumbu, Mfwangano, Songhor, Koru) and Uganda (Napak).

DESCRIPTION.

Upper molars. (Text-figs. 1C, 2, 3A.)

Associated upper molars are present in six specimens : all three molars are preserved in the holotype, though fairly heavily worn ; in R137.49* M^1 is well preserved, and M^2 and M^3 are badly broken ; R483.51 and R1382.51 contain M^1 and M^2 in association ; M14203 and an un-numbered specimen from site R31 contain M^2 and M^3. In addition there are 14 fairly complete isolated molars and a number of fragments.

The following measurements were made wherever possible:—(1) the greatest anteroposterior length, (2) the transverse width perpendicular to (1), (3) the anterior oblique width across the parastyle and protocone, (4) the posterior oblique width across the mesostyle and hypocone. (Tables I and II). When the results were plotted on probability paper (Harding 1949) it was found that the specimens did not form a unimodal population : five specimens, containing 7 molars, formed a secondary grouping near the upper limit of the range of variation. It is therefore possible to distinguish a large form from the typical form of the species. The following specimens are referred to the large form :—

R483.51 (M^1, M^2) from Kiahera, Rusinga.
R411.48 (M^1) from the top of Kiahera Hill, Rusinga.
M14202 (M^3) from Koru.
R1382.51 (M^1, M^2) from Hiwegi, Rusinga.
R533.51 (M^3) from Kamasengere, Rusinga.

The first three of these sites have also yielded upper molars of the typical form so that the difference cannot be due to geological age. The disproportion in numbers (29 teeth of the typical form : 7 of the large form) disfavours a sexual difference. It is possible that two closely related species were present, differing in their ecology : the large form may have occupied a habitat where it was less liable to fossilisation. However, as morphological distinctions between the two forms are very slight, and wide variations in size are known in other chalicotheres, such as *Phyllotillon betpakdalensis* (Borissiak 1946), it is not proposed at present to give the large form a distinct specific name.

M^1 is much the smallest of the three molars. Its length usually slightly exceeds the transverse width, but the length/width index ranges from 93 to 107. The apparent length is frequently reduced by wear of the metastyle and flaking away of the enamel on the anterior border.

The outline of the base of the tooth might be described as a quadrilateral with rounded apices. There is a bay, varying in depth, somewhat anterior to the middle of the buccal side. The posterior side is convex, reaching its greatest prominence near the mid-point. The anterior side is also convex, but it recedes lingually, so that the lingual side is much shorter than the buccal side. There is a slight bay in the lingual side, situated more posteriorly than the buccal bay. The anterior oblique width is approximately equal to the posterior oblique width (index, anterior/posterior width, 97–108).

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*Specimen numbers beginning R, Sgr or MFW are field numbers indicating locality (Rusinga, Songhor or Mfwangano respectively) and year of collection. These specimens are the property of the National Museum of Kenya, Nairobi. Registration numbers of National Museum of Kenya, Nairobi specimens begin with F, those of the British Museum (Natural History) with M.

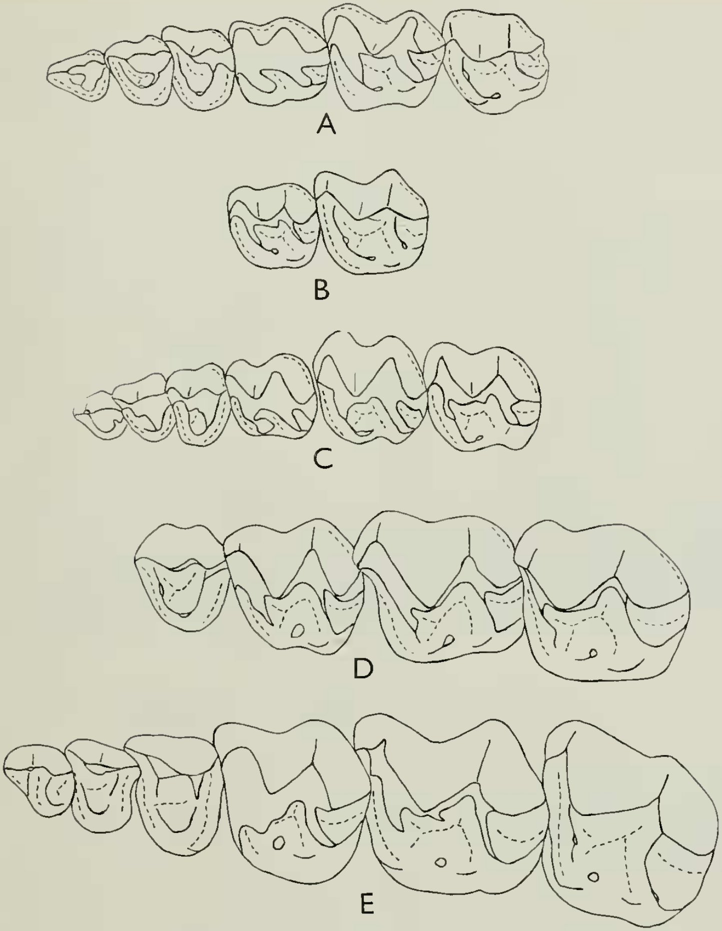

FIG. 1. Upper cheek teeth. A. *Schizotherium priscum*, from specimens in the Paris Museum. B. *Chalicotherium pilgrimi*, M^1 and M^2, BMNH. M12166. C. *C. rusingense*, holotype. D. *C. grande*, P^4–M^3, from cast, BMNH. M40821. E. *C. goldfussi*, from cast of Nikolsburg specimen, BMNH. M12154. All × $\frac{1}{2}$.

There are three roots. The buccal roots correspond to the two lobes of the buccal outline ; in cross-section they are oval, with their long axes transverse to the tooth. The lingual root is extended in an anteroposterior direction, and is partly divided by grooves on its buccal and lingual surfaces into anterior and posterior moieties, corresponding to the lobes of the lingual outline. The buccal roots taper apically ; their nearly perpendicular buccal surfaces are situated near the surface of the maxilla. In four specimens in which M^1 is implanted in the bone their length ranges from 16·3 to 20 mm., the anterior root being apparently slightly longer than the posterior. The lingual root is more frequently preserved in isolated teeth, in which its length is 11·3–14·5 mm. It is stouter than the buccal roots and less tapering. It is inclined lingually, diverging from the buccal roots. The base of the tooth between the roots is flat, and in well-preserved specimens it is crossed by three inter-radicular crests which arise from the inner sides of the roots and meet in the centre of the base.

TABLE I.

Measurements (mm.) of teeth of *Chalicotherium rusingense*, holotype.

	Length	Transverse	Oblique width	
			Anterior	Posterior
M^3	26·3	25·0	27·0	23·1 e
M^2	27·6	25·0	24·6	24·8
M^1	20·5	19·3	19·0	19·5
P^4	13·0	17·8		
P^3	12·3	14·2		
P^2	10·0	9·5		

The crown is dominated by the W-shaped ectoloph, formed from the paracone and metacone. These cusps are approximately equal in height. Their tips are placed near the mid-line of the crown, their lingual surfaces are nearly vertical, and their buccal surfaces are inclined at about 40° to the plane of the base of the tooth. Both cusps are V-shaped in crown view, but the arms of the metacone are much more divergent than those of the paracone, as the posterior arm runs directly backwards (on little-worn teeth) to the mid-posterior prominence of the outline. A ridge runs down the buccal slope of the paracone, and a similar but fainter and shorter ridge is sometimes present near the tip of the metacone. The ectoloph is buttressed by the parastyle and mesostyle, which are situated on the two lobes of the buccal margin, and are almost as high as the paracone and metacone. Unworn specimens of M^2 and M^3 show that the tips of the parastyle and mesostyle do not lie in the ectoloph, but are joined to it by transverse crests ; this is probably also true of M^1, but sufficiently unworn specimens of this tooth are unknown. Seen from the buccal side, the mesostyle (and presumably also the parastyle, which has suffered damage on all the specimens of M^1) thickens towards the base. In two of the three specimens of M^1 referred to the large form a swelling is present about half-way up the anterobuccal face of the mesostyle ; it is not present in the typical form. The buccal cingulum is very indistinct, least so externally to the metacone ; where it joins the posterior crest of the metacone a rudimentary metastyle is formed.

The ectoloph wears on its lingual surface and so becomes displaced towards the buccal side of the crown in worn specimens. The posterior crest of the metacone becomes rotated buccally and the angle between the arms of the metacone V is thus reduced. Tongues of exposed dentine extend to the tips of the parastyle and mesostyle, so that in very worn teeth the styles are hardly distinguishable from the ectoloph itself.

The protoloph and metaloph branch off from the anterior arms of the paracone and metacone respectively, and run obliquely backwards, parallel to the anterior border of the tooth. Their anterior surfaces are nearly vertical, their posterior surfaces much less so. The protoloph is short, extending only to the protoconule which is placed close to the lingual side of the paracone. The protocone is situated above the anterior lobe of the lingual margin, and more posteriorly than the protoconule, from which it is separated by a valley. The protocone is subequal in height to the protoconule, and much lower than the paracone. It has the form of a cone, tilted lingually so that its lingual surface is nearly vertical, and developed into a ridge anteriorly. In four specimens a low but distinct crest arises on the lingual side of the protoconule, crosses the intervening valley and joins the anterior ridge of the protocone ; the crest is absent in five other specimens. The metaloph rises at its lingual end to form the hypocone, which is somewhat higher than the protocone and placed a little less lingually on the crown. There is no trace of a metaconule.

The anterior border of the crown is occupied by a broad cingulum, its edge formed by a sharp marginal crest which branches off from the ectoloph lingually to the parastyle. This crest rises in front of the protoconule ; farther lingually it falls rapidly and merges into the anterolingual side of the protocone. There is no distinct cingulum lingually to the protocone. A posterior marginal crest arises from the tip of the hypocone, enclosing with the metaloph and metacone a triangular basin (postfossette). In seven out of ten specimens this basin is interrupted by a small transverse crest that branches off the lingual side of the ectoloph. Owing to wear, details of the central basin cannot be determined.

TABLE II.

Dimensions of upper molars, *C. rusingense.*

		Typical form				Large form	P (t-test)
		N	m	s	Range (mm.)	Measurements (mm.)	
Length	M^1	7	19·7	0·78	19·0–20·8	21·7, 22·7	< ·01
	M^2	7	25·5	1·30	24·4–27·6	28·9, 29·3	< ·02
	M^3	5	24·9	0·98	24·0–26·3	26·2, 26·5	> ·1
Transverse width	M^1	9	19·1	0·82	18·0–20·3	21·7, 22·0, 22·4	< ·01
	M^2	10	24·7	0·92	23·0–26·5	28·5	< ·01
	M^3	6	24·0	1·02	23·3–25·2	27·0, 27·1	< ·02
Oblique width (parastyle-protocone)	M^1	7	19·7	0·61	18·8–20·3	22·5, 23·0	< ·01
	M^2	6	25·8	1·04	24·6–27·2	30·8, 31·0	< ·01
	M^3	5	26·2	0·57	25·6–27·0	28·6, 30·3	< ·01
Oblique width (mesostyle-hypocone)	M^1	9	19·8	0·81	18·4–20·9	21·4, 21·9, 22·5	< ·01
	M^2	10	23·9	1·00	22·1–25·2	27·5	< ·01
	M^3	8	22·1	0·61	20·6–23·1	23·8	< ·05

The last column gives the probability (obtained by a t-test) that the means of the large form fall within the range of variation of the typical form.

M^2 is about 30% larger than M^1 in all dimensions. The posterior lobe of the lingual edge is less developed, the lingual bay being situated relatively more posteriorly. In correlation with this, the posterior moiety of the lingual root is proportionately smaller, and the hypocone, though not reduced in height, occupies a smaller proportion of the lingual border of the crown. The metacone is lower than the paracone when unworn, and it occupies a smaller proportion of the ectoloph. The index, anterior oblique width/posterior oblique width ranges from 101 to 113.

The variations observed in M^1 are also present in M^2. The bay in the buccal outline varies in depth. The swelling on the anterobuccal face of the mesostyle occurs in the only specimen of the large form in which this region is preserved, but it also occurs in a specimen of the typical form (R689.49) ; it is absent in four other specimens. The crest joining the protoconule to the protocone is present in seven specimens (including one of the large form) and absent in three (one of the large form) ; it is particularly strongly developed in M14203 (the smallest specimen). The small transverse crest in the postfossette is present in six specimens and absent in four. In R689.49 the buccal roots are kidney-shaped in cross-section, owing to a groove on the internal side of each root ; this variation does not occur in six other specimens, and it was not observed in M^1.

Five specimens of M^2 are practically unworn, revealing details of the central basin that could not be seen on M^1. Between the protocone and the hypocone is a flattened area demarcated lingually by a marginal ridge. A small crest (crista) passes backwards from the paracone down the lingual side of the ectoloph to the deepest part of the central basin ; it is visible in all five specimens. In M 14203 another crest (crochet) passes down the anterior face of the metaloph to end in the central valley opposite the base of the crista. A trace of this is present in R 929.50, which is more worn, but it is absent in four unworn specimens. A trace of the crochet appears to be present in two specimens of M^1 (R 496.50 and R 12.48).

M^3 is very nearly of the same length, width and height as M^2. It differs however in proportions. The posterior part of the crown is shorter in proportion to the anterior part, and also narrower (anterior/posterior oblique width index 115–121). The posterior buccal root is displaced lingually in relation to the anterior buccal root. The anterior of the two buccal roots is slightly longer than the posterior (visible in two specimens), which is of about the same length as the lingual root. The lobe of the outline that bears the hypocone is less prominent than on M^2, and the bay in the lingual border is very slight, though the partial subdivision of the lingual root resembles that of M^2. The protocone is placed relatively farther back on the crown, and the hypocone is a little nearer to the posterior edge and less lingual than in M^2. The metacone is much lower than the paracone and slightly lower than the mesostyle. It is situated quite near to the posterior border of the crown, and its posterior arm is short.

M^3 varies in the same ways as the other molars. The bay in the buccal edge varies in depth. The mesostyle never shows the basal swelling. The crest joining the protoconule to the protocone is absent in only one specimen and present in eight ; in M 14203 it is as strongly developed as on M^2. The crista is present in six specimens, definitely absent in one and probably absent in another specimen. The crochet is present in M. 14203 and probably two other specimens. The transverse crest in the postfossette is present in only one out of eight specimens.

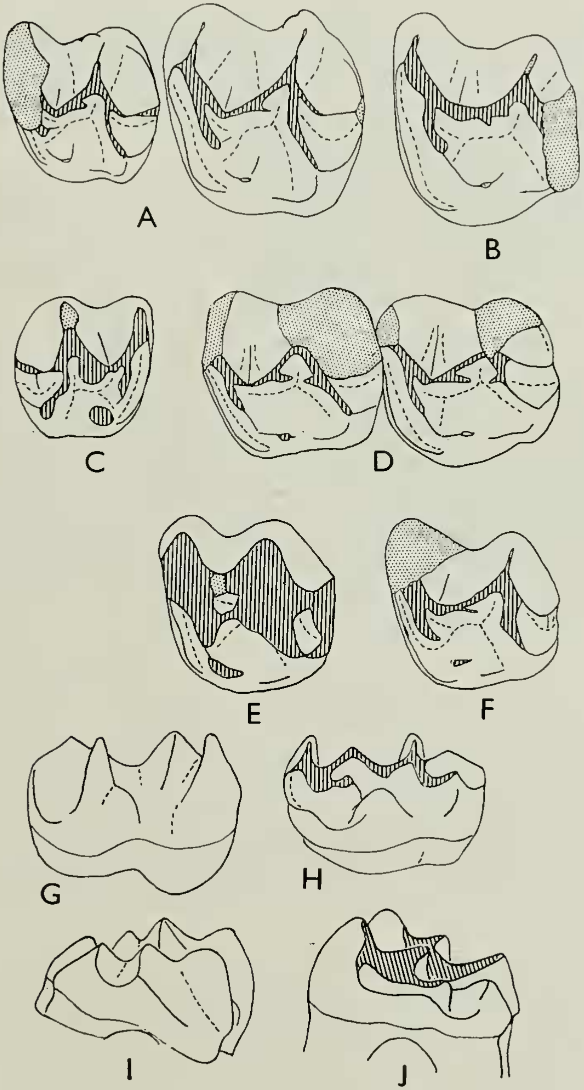

FIG. 2. Upper molars of *Chalicotherium rusingense*. A. Left M^1 and M^2, R 1382.51. B Left M^3 from Koru, BMNH. M14202. C. Right M^1, R909.47. D. Left M^2 and M^3 from Koru, BMNH. M14203. E. Left M^2, worn, from site R 91. F. Left M^3, from site R 38. G–J. Left M^2, R 1382.51, buccal, lingual, posterior and anterior views. All × 1.

Specimens M 14202 and R 533.51 stand apart from the others in their greater breadth, and are considered to belong to the large form, even though they are not significantly greater in length. M 14202 fits with M_3 of R 1782.50, which is also believed to belong to the large form (see below).

Comparisons. (Text-fig. 1). Upper molars of the typical form of *C. rusingense* are only about 60% as large as those of typical *C. grande* from Sansan, but are similar in size to those of *C. pilgrimi.* Molars of *Schizotherium priscum* resemble in size those of the large form of *C. rusingense* ; M^1 of *S. turgaicum* (Borissiak 1921) is smaller than in *C. rusingense* (17·5 × 17 mm.).

The length/width indices of the upper molars of *C. grande* (M^1 103–109, M^2 104–111, M^3 93–109) are not significantly different from those of *C. rusingense* (M^1 93–107, M^2 100–110, M^3 97–107), and in *C. pilgrimi* M^2 has an index of 106. In *Schizotherium priscum* M^2 and M^3 are typically a little narrower (indices 110–115), but there is less difference in M^1 (indices of two specimens 98 and 112).

In *C. rusingense* M^2 is larger in comparison with M^1 than in *C. grande, C. pilgrimi* or *S. priscum.* Indices of comparable measurements on the two teeth show the following ranges : *C. rusingense* (3 specimens) 127–138, *C. grande* (3 specimens) 114–131, *C. pilgrimi* (1 specimen) 112–130, *S. priscum* (2 specimens) 113–127.

C. rusingense resembles *C. grande* in the displacement of the paracone and metacone from the buccal side of the crown. In *C. pilgrimi* and *S. priscum* these cusps are more buccal in position, and their buccal slopes are steeper. Moreover, in the two latter species the protoconule is placed about equidistant from the tips of the paracone and the protocone, whereas in *C. rusingense* and *C. grande* it is nearer the paracone.

In all known specimens of *S. priscum* the protoloph continues over the tip of the protoconule to the tip of the protocone, although between these cusps it dips to form a notch. The same condition is found in *C. pilgrimi.* In the other species of *Chalicotherium* the connection between the protoconule and the protocone is frequently broken, less often in *C. rusingense* than in *C. grande.* The connection is complete in a large specimen of *C. grande* from Cournon, but in six individuals from Sansan that part of the crest which passes up the anterior slope of the protocone is very weak or completely absent. In *C. rusingense* this part of the crest is retained, and it is the crest on the lingual slope of the protoconule that disappears when the connection is broken.

The crista is present on all molars of *S. priscum* that are sufficiently unworn, and it is also present on M^1 and M^2 of the holotype of *C. pilgrimi.* It occurs in the majority of specimens of *C. rusingense* and *C. grande,* but is sometimes absent. The crochet is much less common. It was not observed in *S. priscum, C. pilgrimi* or *C. grande,* but is present in a few specimens of *C. rusingense,* and Wehrli (1929) recorded its presence in one specimen of M^2 of *C. goldfussi.* The small rib on the lingual side of the ectoloph in the postfossette is present on all known molars of *S. priscum* ; in *C. rusingense* it is much more common on M^1 than on M^3 ; in *C. salinum* it occurs on the holotype M^3. It is uncommon in *C. grande* where it was found in only one specimen (M^2 and M^3), and Wehrli (1929) noted it in a few specimens of M^3 of *C. goldfussi.* It is not present on M^1 or M^2 of the holotype of *C. pilgrimi.*

The rib on the buccal slope of the paracone is present in all specimens of *C. rusingense* and *S. priscum.* It is also present in *C. pilgrimi* and *C. salinum,* but it is weaker and sometimes absent in *C. grande* and *C. goldfussi. S. priscum* differs from the species of *Chalicotherium* in possessing traces of a buccal cingulum between the parastyle and the mesostyle.

The upper molar roots of *C. grande* have not been described and are not visible in material that I have examined. The lingual root of *C. goldfussi* (one of Kaup's specimens, seen as a cast) and the three roots of M^3 of *Nestoritherium sinense* are very much like *C. rusingense.* In two specimens of M^3 of *S. priscum* at Paris a small supernumerary root is present, immediately to the lingual side of the anterobuccal root ; this was not observed in *C. rusingense.*

Upper Premolars (Text-figs. 1C, 3)

The three premolars are preserved together only in the holotype : in addition there are 31 isolated teeth of which only one (R12.48) may definitely be identified as P^2. As P^3 and P^4 resemble each other in morphology, and differ only in size and proportions, the overlap of their ranges of variation makes it impossible to identify every specimen with certainty. By plotting the lengths or widths on arithmetical probability paper (Harding 1949) the presence of two types of teeth in the collection, in nearly equal numbers, was confirmed, and the mean dimensions and standard deviations of P^3 and P^4 could be estimated. (Table III.)

In the holotype the total length of the premolar series is 38 mm., or 51% of the length of the molar series.

TABLE III.

Upper molars of *C. rusingense,* inclusive of large form.

	Length				Width			
	N	m	s	V	N	m	s	V
M^3	7	25·3	1·07	4·2	8	24·8	1·65	6·7
M^2	9	26·5	1·85	7·0	11	25·0	1·48	5·9
M^1	9	20·4	1·25	6·1	12	19·9	1·47	7·4
P^4	21	13·2	0·76	5·8	21	18·1	1·10	6·1
P^3		11·5	0·53	4·6		14·7	1·04	7·1
P^2	2	9·7	—	—	2	9·2	—	—

The width of P^4 of the holotype is 92% of that of M^1, but it is much shorter, its width/length ratio being 1·37. In the largest of the isolated premolars the width/length ratio reaches 1·44. P^3 of the holotype is a little shorter than P^4

and much narrower : its width/length ratio is 1·16. The narrowest of the isolated specimens identified as P^3 has a ratio of 1·12.

The buccal edge of P^4 and P^3 usually shows a slight bay. The posterior edge is evenly convex, reaching its most posterior point at the metastyle, to the buccal side of the middle line of the tooth. The lingual edge is evenly rounded, but the anterior buccal apex is the most acute of the three apices of the outline. The anterior edge is straighter than the posterior one, and recedes posterolingually, especially in teeth referred to P^3. Owing to wear or breakage of the parastyle and metastyle the anterior and posterior borders of isolated teeth often appear nearly parallel.

There are normally two roots, one anterobuccal in position and circular in section, and the other a broad, flattened structure which extends along the posterior side of the tooth. The posterior root appears to represent the lingual and posterobuccal roots fused together. In two specimens these roots are separate, so that there are three equal roots. In two others, both the buccal roots have united with the lingual root to give a single root, V-shaped in cross-section, having a deep cleft on its buccal side.

The ectoloph, consisting of parastyle, paracone and metacone, occupies the buccal half of the crown. The parastyle is situated farther buccally than the paracone, more so on P^4 than on P^3. There is no mesostyle, and the buccal cingulum is vestigial or absent. The buccal surface of the ectoloph is steeper than on the molars ; a rib usually runs down it from the tip of the paracone, as on the molars. The metacone is lower than the paracone, the two cusps being separated by a notch worn by the hypoconid of the lower premolar. As completely unworn premolars have not been found, it is uncertain how far the apparent apex of the metacone is an artefact due to the cutting of the notch. In P^3 of the holotype and in some isolated teeth the notch is weakly developed, and the metacone then appears as an angulation situated rather high up on the posterior side of the paracone. P^3 possesses an important area of wear on the lingual side of the posterior part of the ectoloph, due to the anterior part of the trigonid of P_4. The corresponding wear on P^4 is small, and develops rather late in the life of the tooth. Accordingly, the metacone appears to stand farther forward on P^3 than on P^4.

In lightly worn teeth the protoloph is seen to join the ectoloph midway between the paracone and the parastyle, as in the molars, but in severely worn teeth the protoloph appears to arise directly from the paracone. The protocone of the molar is represented by the deuterocone of the premolar, a stout cusp, flattened on its buccal side and crested anteriorly. It is linked to the metacone by the metaloph, but is separated from the protoconule by a valley. As on the molars, this valley is frequently crossed by a crest that arises from the protoconule. This crest is distinct in the holotype and in eleven of the isolated teeth ; it is absent or very weak in 13 of the isolated teeth. There is no hypocone on P^4 or P^3. The anterior and posterior borders of the crown are occupied by prominent cingula, elevated near the middle line of the tooth. In M 14221 (P^3) the posterior cingulum continues as a ridge up the posterior surface of the deuterocone, but in other specimens this ridge is indistinct or absent, and the cingulum ends at the base of the deuterocone.

There is no lingual cingulum. In the least worn specimens a crista can be seen on the posterolingual side of the paracone. In two specimens a short ridge, probably corresponding to the crochet of the molar, extends into the central basin from the metaloph ; it is absent in five other specimens.

The two specimens of P^2 are both rather severely worn. The crown is triangular, slightly longer than broad, with the lingual apex situated near the posterior end. In the holotype, P^2 has 81% of the length of P^3. The isolated specimen has two roots, arranged like those of typical specimens of P^3 and P^4. In both specimens the parastyle is low and weak, and the paracone is placed in the anterior half of the crown, but no metacone can be distinguished, perhaps due to wear. There is no buccal cingulum. The buccal slope of the paracone bears a vertical rib. The whole of the lingual face of the ectoloph posterior to the paracone is occupied by a large area of wear produced by P_3. Owing to wear, details of the lingual part of the crown are obscure. The deuterocone seems to be placed rather far back on the crown, and to have taken part in the formation of a metaloph, like the hypocone of the molar. The protoloph is probably reduced or absent. A posterior cingulum is present.

Comparisons (Text-fig. 1). In *Schizotherium priscum* the premolars are larger in comparison with the molars : the length of the premolar series is about 56% of that of the molar series, compared with 51% in *C. rusingense.* I have been unable to find a complete upper cheek dentition of typical *C. grande*, but in the type of *C. grande rhodanicum* (from Depéret's figure) the percentage is 45, and in the Nikolsburg specimen of *C. goldfussi* figured by Abel (1922) it is 42.

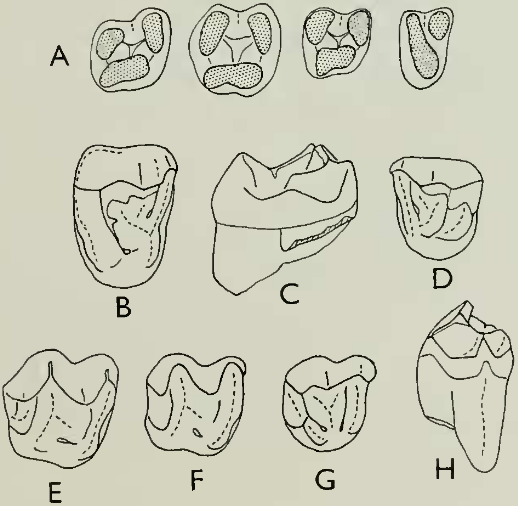

Fig. 3. *Chalicotherium rusingense.* A, basal view of P^4–M^3 to show arrangement of roots. B, right P^4, R 485.51, crown view. C, the same, anterior view. D, left P^3, from Koru, BMNH. M14221, crown view. E, F, right milk-molars, R 269.48 and R 65.50. G, H, abnormal premolar from Napak, crown view and anterior view. All × 1, except A × ½.

In *S. priscum* P^3 is more equal to P^4 (length index P^3/P^4 in two specimens of *S. priscum* 93 and 104 ; in the holotype of *C. rusingense* it is 89). In *C. grande* this index ranges from 87 (Crusafont & Villalta 1942) to 85 (measured from the figure of Depéret 1892); in the Nikolsburg specimen of *C. goldfussi* it is 82.

Differences in the pattern of P^4 are slight. They concern mainly the protoloph which in *Schizotherium* continues to the tip of the deuterocone, whereas in *Chalicotherium* it tends to be interrupted, probably in correlation with the protoloph of the molars. In *Schizotherium* P^3 is similar to P^4 in pattern, differing only in being slightly narrower. In *C. rusingense* P^3 is more definitely narrower, with a more oblique anterior edge, but its pattern still resembles that of P^4. In *C. grande, C. goldfussi* and *C. brevirostris* there is a further distinction in that the protoloph of P^3 is lower in relation to the ectoloph.

The alveoli in a maxilla of *C. grande* in Paris show that P^3 and P^4 each possessed a broad posterior root and a smaller anterobuccal root, as in *C. rusingense.* This is also true of Spanish specimens (Villalta & Crusafont 1943).

P^2 of *Schizotherium priscum* has a distinct protoloph, which branches from the ectoloph between the parastyle and the paracone and runs to the tip of the protocone as in P^3. In *C. grande* (Crusafont & Villalta 1943) the protoloph is weakly developed. *C. rusingense* seems to approach *C. grande* in this respect. The teeth of *C. grande* identified by Wegner (1913) as P^1 and P^2 are probably P^2 and P^3 respectively.

? Abnormal specimen of P^3. (Text-fig. 3G, H.)

An upper premolar from Napak measures 12 × 14 mm. (width/length ratio 1·17). It differs from upper premolars of *C. rusingense* in the presence of a groove on the posterolingual surface of the lingual root (which is fused with the posterobuccal root), associated with a nick in the posterolingual enamel border. The ectoloph shows the normal pattern of P^3, but there are differences in the lingual part of the crown. The protoloph extends to the lingual side of the crown, and ends in a protoconule placed immediately anterior to the deuterocone. The metaloph forks : its anterior branch runs to the tip of the deuterocone, and the posterior branch interrupts the posterior cingulum, above the nick in the enamel border. The anterior cingulum ends lingually at the base of the protoconule.

A similar tooth from the Upper Miocene of Steinheim was referred by von Koenigswald (1932) to *Metaschizotherium bavaricum*, and another specimen with the same characters was described by Roger (1885). These European teeth are much larger and more transverse than the Napak specimen. It is possible that this represents an African species of *Metaschizotherium* (i.e. *Phyllotillon*), as I suggested in an earlier report (Butler 1962), but in the absence of other evidence for the existence of *Phyllotillon* in Africa it now seems to me preferable to interpret it as an abnormal P^3 of *Chalicotherium rusingense.*

Upper milk-molars. (Text-fig. 3E, F.)

Some isolated upper molariform teeth of small size are probably milk-molars. R 269.48 is tentatively identified as Pd^4. It measures 16 × 15·5 mm. It is lightly worn. The bay in the buccal edge is situated more anteriorly than in M^1 ; the lingual root tapers markedly towards the tip and is nearly equal in length to the anterior buccal root. As on some specimens of M^1, the protoconule is connected to the anterior side of the protocone by a low but distinct crest, and there is a small cross-crest in the postfossette.

R 65.50 is much smaller (13·5 × 14 mm.) and is possibly Pd^3. It is rather severely worn, and its unworn length would be greater. The roots are broken off, but the crown appears to be similar to R 269.48.

A third specimen, R 631.47, measures 19 × 18·5 mm., approaching the lower limit of size of M^1. Its lingual root resembles that of M^1, but the anterior border of the tooth is more oblique. This could be either an abnormally small M^1 or an example of Pd^4 of the large form. An incomplete specimen, R 697.51, is similar in size.

If the identification of these teeth is correct, it would follow that the milk-molars of *C. rusingense* are larger in comparison with M^1 than in *C. grande*, where Pd^4 is about 65% and Pd^3 about 55% as long as M^1 (Villalta & Crusafont 1943). In *Schizotherium priscum*, to judge from the figure of Stehlin (1905), the milk-molars are less reduced than in *C. grande* and may have resembled those of *C. rusingense* in relative size.

In shape, however, the milk-molars of *S. priscum* are narrower, especially Pd^3. Those of *C. grande* and *C. wetzleri* are more like *C. rusingense*. The small crest in the postfossette occurs in *S. priscum*, and also in the supposed Pd^4 of *C. grande rhodanicum* (Depéret 1887).

Lower molars. (Text-figs. 4, 5 ; Tables IV, V, pp. 190, 191.)

The mandible F3608 contains all the molars of both sides, in R 410.55 the right series is preserved in a mandible fragment, and R 1782.50 consists of a collection of separate cheek teeth from the right side which probably belong to one individual. M_1 and M_2 of R 1782.50 are considerably larger than those of the other two specimens, and fit upper molars referred to the large form. Seven other specimens show single teeth or parts of two adjacent teeth in mandible fragments, permitting identification. There are also six fairly complete isolated lower molars (including one specimen from Napak) and numerous fragments, consisting mostly of isolated trigonids or talonids.

The three complete sets show that M_1 is only 73–77% as long as M_2. It is however, proportionately wider : the trigonid width is 58–62% of the length of the tooth, compared with 53–55% in M_2. Only one mandible fragment (R 520.48) is identified as containing M_1 ; the tooth is broken anteriorly, but its talonid agrees closely with M_1 of R 1782.50, and it is therefore referred to the large form. There is also an isolated talonid of the typical form (R 68.49).

Six specimens contain M_2 or M_3 with a fragment or alveolus of an adjacent molar, permitting identification. These, together with the specimens showing the complete molar series, show that in the typical form M_2 (4 specimens) ranges in length from 23·4–24·6 mm., and M_3 (4 specimens) from 24·4–26·8 mm. In F 3608 and R 410.55 M_3 is about 3 mm. longer than M_2. M_3 is longer in proportion to its width (across the trigonid) than M_2. In R 1782.50 the difference in length is only 0·4 mm., and it would appear that, as in the upper dentition, the last molar of the large form is proportionately shorter, though its width exceeds that of the typical form.

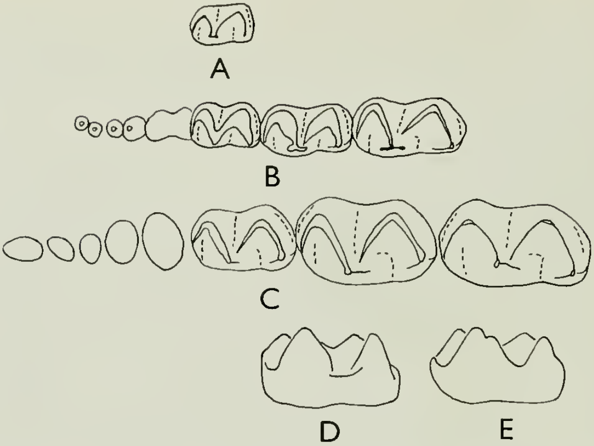

Fig. 4. Right lower molars of *Chalicotherium*. A, *C. pilgrimi*, M_1, BMNH. M12167. B, *C. rusingense*, Rusinga, F 3608. C, *C. grande*, Paris specimen from Sansan (left teeth reversed). D, *C. grande*, lingual view of M_2, BMNH. M40821. E, *C. styriacum*, lingual view of M_2, from cast, BMNH. M12112. All × $\frac{1}{2}$.

Some of the isolated molars, and all the incomplete teeth, cannot be definitely sorted into second and third molars. Recourse was therefore made to probability paper, by which means and standard deviations could be estimated, assuming equal numbers of M_2 and M_3 in the collection.

Altogether, 5 independent specimens containing lower molars are referred to the large form, as against 22 referred to the typical form.

The three molars are so much alike that a single description will suffice for all. There are two roots, flattened from front to back and inclined somewhat posteriorly. The posterior root is the stouter of the two, especially in M_3, where its posterior surface is more rounded. The length of the roots on M_2 and M_3 is 20–24 mm. A low inter-radicular crest is present on the base of the tooth.

Of the two V-shaped buccal cusps, the protoconid is a little lower than the hypoconid and occupies a smaller area on the crown. The anterior crest of the protoconid falls rapidly as it passes in a curve along the anterior border of the crown, and at its lingual end it becomes a cingulum ledge anterior to the base of the metaconid. There is no paraconid, though a notch may be worn in the crest to give the appearance of that cusp. A narrow cingulum on the anterior edge of the crown does not extend to the buccal side of the protoconid. The posterior arm of the protoconid remains nearly horizontal, crossing the crown to join the metaconid. The latter cusp is higher than the protoconid ; its base extends forward so as partly to close the trigonid basin. Closely applied to the posterior surface of the metaconid is the metastylid, the tip of which is lower than that of the metaconid. In three specimens the metastylid is represented only by a sharp posterior crest of the metaconid. The arms of the hypoconid diverge at a greater angle than those of the protoconid. The anterior arm ends between the metaconid and the metastylid, so that the latter cusp projects backwards partly closing the talonid basin. The posterior arm of the hypoconid runs to the tip of the entoconid, a conical cusp, somewhat lower than the metaconid, and placed at the posterolingual corner of the crown. The trigonid basin opens lingually anteriorly to the base of the metaconid, and the trigonid basin opens between the metastylid and the entoconid. The posterior edge of the crown is occupied by a cingulum, somewhat variable in development. When best developed it rises towards the lingual side to form a vertical rib on the posterior face of the entoconid ; this rib represents the hypoconulid.

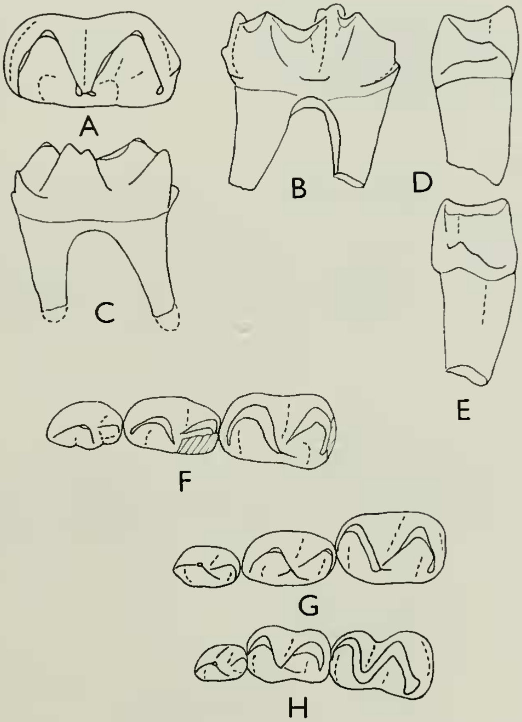

Fig. 5. A–E, Right M_3 of *Chalicotherium rusingense* from Rusinga, × 1, A, crown view ; B, buccal view ; C, lingual view ; D, anterior view ; E, posterior view. F, lower premolars of *C. rusingense*, R 1782.50 × 1. G, M_1–P_3 of *C. grande*, BMNH. M40821 and (P_3) a Paris specimen, × ½. H, M_1–P_3 of *C. goldfussi*, from cast, BMNH. M2719, × ½.

The effect of wear is to expose a strip of dentine on the crests of the protoconid and the hypoconid. These cusps are thus reduced in height. The metaconid and entoconid however are worn mainly on their buccal sides, and their height is reduced more slowly.

Comparisons. The lower molars of *C. rusingense* are much smaller than those of *C. grande* or *C. wetzleri*, but a little larger than those of *C. pilgrimi*. Typical specimens are similar in size to those of *Schizotherium turgaicum* and somewhat smaller than those of *S. priscum*.

In *Schizotherium* the hypoconulid of M_3 is enlarged to form a posterior heel, probably the relic of a larger structure present in Eomoropinae. In *C. rusingense*, as in *C. grande* and other species of *Chalicotherium*, M_3 resembles M_2.

The metastylid is distinctly developed in *Schizotherium*, as well as in *C. pilgrimi*, *C. wetzleri* and (with a few exceptions) in *C. rusingense.* In *C. grande* and other late species it is more or less merged into the metaconid.

The width/length index of the lower molars is somewhat greater in *C. grande* (56–58 in specimens of M_2 from Sansan) than in *C. rusingense* (M_2 : 53–55). Wehrli's (1939) measurements show that in *C. goldfussi* still broader molars can occur (M_2 : 55–62). Comparatively narrow molars (index of M_2 below 55) occur in *C. wetzleri*, *C. pilgrimi* and species of *Schizotherium*.

Molar Occlusal Relations. (Text-fig. 6.)

The functional inter-relations of the upper and lower molars were studied by examining the wear facets and by fitting teeth together.

In the centric position, in which the teeth are pressed together as closely as possible, the lower molar covers the lingual part of the upper molar, the inner borders of both teeth being in line. The inter-relations of the cusps in the centric position may be tabulated as follows :—

Hypoconid tip	Centre of central valley, between tips of paracone and metacone.
Protoconid tip	Cingulum anterior to the protoconule.
Entoconid	Groove between protocone and hypocone.
Metaconid-metastylid	Space between protocone and the more anterior hypocone.
Paracone tip	Buccal side of tooth, in valley separating protoconid and hypoconid.
Metacone tip	Embrasure between two lower molars, partly filled by posterior cingulum.
Protoconule	Buccal side of metastylid.
Protocone	Between metastylid and entoconid.
Hypocone tip	Against anterior arm of protoconid, in which it wears a notch.

During chewing, the crests of the protoconid and hypoconid slide up the lingual surface of the ectoloph. This can take place only when the lower jaw is displaced to the lateral side of the centric position. The movement was almost certainly ectal, starting when the lower teeth are placed so that the protoconid and hypoconid touch the parastyle and mesostyle respectively ; from this position the lower teeth move medially, upwards and slightly forwards to the centric position.

The facets of wear produced in chewing can without difficulty be homologized with those distinguished in other perissodactyls (Butler 1952).

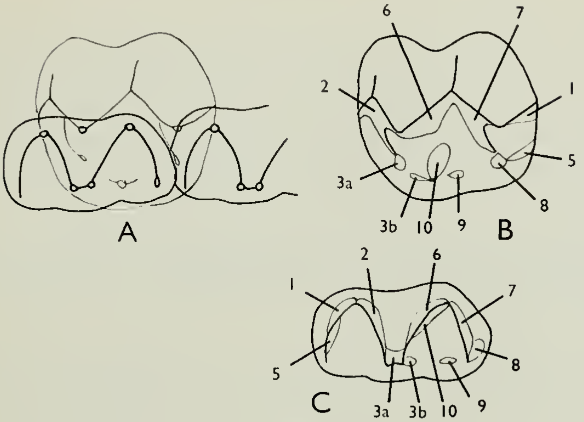

FIG. 6. Molar occlusion of *Chalicotherium rusingense*. A, upper and lower molars superimposed in centric relation. B, C, wear facets on the molars.

	Lower facet	*Upper facet*
1.	Near the edge of the anterobuccal surface of the anterior crest of the protoconid.	Lingual face of the posterior crest of the metacone.
2.	Posterior surface of the protoconid-metaconid crest.	Anterior face of paracone and protoconule.
3.	(a) Buccal surface of metaconid and metastylid, near the tip.	Lingual face of protoconule.
	(b) Posterior face of metastylid, near the tip.	Anterior crest of protocone.
	(These two facets are variable in development, and may be absent, especially 3 (b). When the protocone-protoconule crest is well developed the two facets may unite.)	
4.	(Metaconid-hypocone contact is absent.)	
5.	Edge of anterior crest of protoconid.	Edge of posterior crest of hypocone.
6.	Anterior face of the buccal part of the hypoconid-metastylid crest, near the edge.	Posterolingual face of the paracone- mesostyle crest.
7.	Posterior face of the hypoconid-entoconid crest.	Anterior face of metacone and metaloph.
8.	A posterobuccal facet on the entoconid, involving the vertical rib.	Anterolingual face of hypocone, near its tip.
9.	Anterior surface of entoconid.	Posterior crest of protocone.
	(Contact slight and sometimes absent.)	
10.	Lingual surface of hypoconid.	Buccal surface of protocone.

Of these, 1, 2, 6 and 7 from the main chewing surfaces. Contacts between the lingual cusps (3, 8 and 9) are probably significant only as stops. When the lower jaw swings to the lingual side of the centric position, contacts 5 and 10 would ensure occlusal balance while the teeth on the opposite side of the mouth are in use.

Lower Premolars. (Text-fig. 5.)

Lower premolars are poorly represented in the collection. The mandible F 3608 shows their roots in the left ramus ; three isolated teeth (R 1782.50) probably represent P_2–P_4 of a single individual, but they are in poor condition. Two more worn and isolated teeth (R 738.50 and R 739.50) may be P_3 and P_4 of another individual ; they differ in some respects from R 1782.50 ,and may not be correctly identified. Finally, there is a broken specimen of P_2 (R 12.48).

F 3608 shows that P_1 was absent. The total length of P_2–P_4 is 37 mm., or 53% of the total length of the molars. All the premolars are two-rooted ; their length diminishes from P_4 to P_2.

In R 1782.50, P_4 is shorter and proportionately broader than M_1 (15.5 × 10 mm.). Its roots are flattened anteroposteriorly, but are less distinctly separated at the base than those of the molars. The crown-pattern differs from that of the molars in the following respects : the anterior arm of the protoconid runs in a rather more anterior direction to the middle of the anterior edge of the tooth, where it turns lingually, falling rapidly to form a cingulum that merges into the anterior base of the metaconid ; there is no metastylid ; the hypoconid is much lower than the protoconid, and the crest which connects the hypoconid to the buccal surface of the metaconid is correspondingly low ; the entoconid (broken off) appears to have occupied a smaller proportion of the crown than in the molar, and the posterior cingulum is probably absent.

TABLE IV.

Measurements of lower molars of two specimens of *C. rusingense.*

	F3608			1782.50		
	Length	Trigonid Width	Talonid Width	Length	Trigonid Width	Talonid Width
M_3	26·8	14·0	13·6	26·8	14·4	14·3
M_2	23·8	13·0	12·7	26·4	14·0	13·9
M_1	18·3	10·5	11·5	19·8	—	—

P_3 of R 1782.50 is smaller in all dimensions than P_4 (13 × 9 mm.), and is much less molariform. The anterior arm of the protoconid forms at the anterior end of the crown an angulation that is probably to be interpreted as a small paraconid. The metaconid does not rise to a distinct point, but is united with the protoconid to form a ridge that runs transversely to the crown and slightly backwards. There is no metastylid. The hypoconid is only about half as high as the protoconid, and, though the postero-lingual part of the crown is broken, the entoconid must have been very low and cingulum-like. On P_2 (10 × 6.5 mm.) the protoconid is the only well-developed cusp. An anterior ridge inclined lingually represents the paraconid, and a lingual ridge the metaconid. The talonid is rudimentary. From the small hypoconid a ridge passes forward to merge with the posterobuccal surface of the metaconid ridge. There is a low, cingulum-like entoconid.

R 738.50 differs from P_4 of R 1782.50 in its greater posterior breadth (16 × 11.8 mm.), due to the presence of an accessory cusp on the buccal side of the hypoconid (probably an abnormality). The tooth is very worn, and the presence of a metastylid cannot be affirmed, though it is probable. The entoconid, lower than the hypoconid, stands rather independently from the other cusps. There is no posterior cingulum. R 739.50 (13.3 × 9 mm.) is a specimen of P_3 which agrees with R 738.50 in the presence of a small cingulum cusp buccal to the hypoconid, and it probably comes from the same individual. The entoconid is a small elevation on a cingulum at the posterolingual edge of the crown.

In R 12.48, which is a specimen of P_2, most of the trigonid has flaked away. The hypoconid is even more reduced than in R 1782.50, and the entoconid is represented only by a fragment of cingulum.

Comparisons. The premolar/molar index of *C. rusingense* (53) is close to those of *C. wetzleri* (54 in the Bollingen specimen) and *Schizotherium priscum* (54, from Osborn's figure, 1913) ; it is exceeded by *S.* cf. *avitum* (59, Teilhard de Chardin 1926). In some specimens of *C. grande* the index is reduced (47 in two specimens from Sansan, 44 in a Spanish specimen figured by Villalta & Crusafont 1943).

In *Schizotherium priscum* (Osborn 1912) and *S. turgaicum* (Borissiak 1928) P_4 possesses a weak metastylid, possibly present in one of the specimens of *C. rusingense.* P_3 of *S. priscum* and *S.* cf. *avitum* is more equal to P_4 than in *C. rusingense,* and more similar in pattern ; in *C. grande* P_3 is smaller and simpler than P_4, its metaconid being incompletely differentiated, as in *C. rusingense.* P_2 of *C. grande* is more reduced than in *C. rusingense* ; the metaconid ridge is weak and the roots may fail to separate.

Thus reduction of the premolars has proceeded farther in *C. rusingense* than in *Schizotherium,* but not quite as far as in *C. grande.*

TABLE V.

Dimensions of lower molars of *C. rusingense,* inclusive of large form.

		N	m	s	V
$M_3 + M_2$	Length	17	24·9 mm.	1·75	7·0
	Trigonid width	24	13·4 mm.	0·88	6·6
	Talonid width	20	13·3 mm.	0·54	4·1
				(range)	
M_1	Length	3	18·4 mm.	17·2–19·8	
	Trigonid width	2	10·6 mm.	10·5–10·7	
	Talonid width	3	11·5 mm.	10·7–12·4	

Canines and Incisors. (Text-figs 7, 9.)

In the holotype a diastema of 26 mm. separates P^2 from the upper canine. This is a small, curved tooth, measuring 11·5 × 10·3 mm. at the base of the crown, and

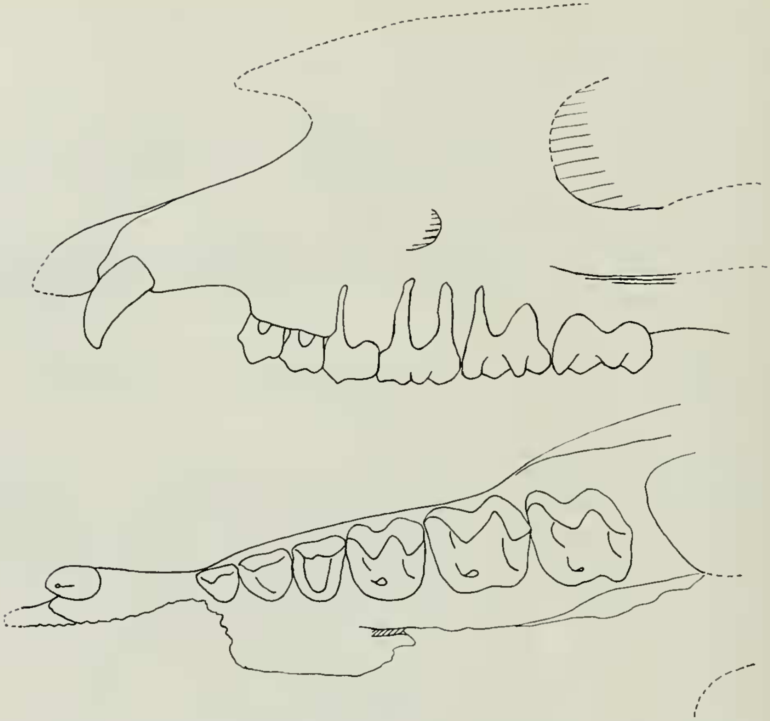

FIG. 7. Partial reconstruction of the face of *Chalicotherium rusingense*, based on the holotype. Side view and palatal view, × ½.

19 mm. from the tip to the posterior border of the alveolus. It is placed procumbently in the jaw, its root making an angle of 60° to the line of the cheek teeth. The tip is blunt. There is a posterior crest near the tip, and a more rounded ridge on the buccal side (corresponding to the rib on the buccal slope of the paracone in the premolars and molars). The lingual surface is poorly preserved, but there was probably a short lingual crest near the tip. The anterior surface is evenly rounded.

Anterior to the canine the alveolar border is preserved for a length of 12 mm., but it contains no teeth. The premaxilla is very slender, and though its tip has been broken off it is unlikely that any upper incisors were present.

In F 3608 and R 283.48 a lower canine root can be seen on either side. The lower canine must have been smaller than the upper canine, measuring in section about 10 × 7 mm. It was procumbent, and was separated from P_2 by a diastema, 26 mm. long in F 3608 and 28 mm. in R 283.48. Three incisor alveoli can be seen on each side of F 3608, immediately anterior to the canine. Their labial walls are broken away, but it is clear that the alveolus for I_2 was the largest.

The incisor from Malembe, Congo Republic, described by Hooijer (1963) as an upper incisor of *Macrotherium* (?) spec., is not referable to *C. rusingense*. It is much too large to fit even into the largest lower incisor alveolus. The molar fragment from Malembe is also much larger than in *C. rusingense* : its talonid width is 25 mm., compared with a mean talonid width of 13·3 mm. for M_2 and M_3 of *C. rusingense*.

Comparisons. The anterior teeth of *Schizotherium priscum* are unknown. An isolated tooth tentatively identified by Teilhard de Chardin (1926) as the lower canine of *S.* cf. *avitum* measures 18 × 9·5 mm. ; this is larger in proportion to M_1 than in *C. rusingense*. The juvenile mandible from St. Gérand-le-Puy described by Filhol (1879) appears to belong to *Phyllotillon*.

A juvenile mandible of *C. grande* from Sansan, figured by Filhol (1891) and now in Paris, shows alveoli for a canine and three incisors. These probably belong to the milk dentition, for gubernacular foramina are present in association with the first two incisors. Id_2 is the largest of the incisors, and the canine is larger than any of the incisors. One of Lartet's specimens of "*Anisodon magnum*" contains the broken alveolus of a lower canine, separated from P_2 by a diastema 29·5 mm. long. An isolated tooth lying shortly anterior to the lower jaw of the skeleton of *C. grande* described by Filhol (1891) may be an incisor (see Viret 1958, pl. 1). Nothing is known of the anterior upper dentition of *C. grande*. A lower milk canine appears to have been present in *C. goldfussi*, if *C. baltavarense* is correctly identified with that species (see p. 168). In *C. brevirostris* upper canine and incisors are absent, as in *Nestoritherium sivalense*.

Face and Palate. (Text-fig. 7 ; Table VI.)

Of the skull, only part of the face and palate are known, mainly from the holotype, but supplemented by fragments of maxilla.

Anterior to M^1 the length of the face is 1·23 times the length of the upper molar series. The external narial opening extends back to above P^3 ; it is flanked by a slender process of the small premaxilla. The zygomatic process arises above the posterior end of M^2, and the anterior end of the orbit was probably situated above the anterior part of M^3. The infraorbital foramen is preserved only in R 483.51, where it opens above M^1. In other specimens the floor of the infraorbital canal can be traced back to the orbit. The canal and the foramen are situated fairly high on the face, about 25 mm. above the alveolar border of the cheek teeth. The maxillary sinus is represented by a small cavity between the infraorbital canal and the roots of the molars.

TABLE VI.

Measurements of face and palate, *C. rusingense*, holotype.

Antemolar length	123 mm.
Length diastema	22 mm.
M^1–M^3 inclusive	75 mm.
P^2–P^4 inclusive	38 mm.
C–P^4 inclusive	80 mm.
Infraorbital foramen—alveolar border	32 mm.
Lower edge of orbit—alveolar border	41 mm.
Height of zygoma	30 mm.
Width of palate between first molars (est.)	58 mm.

The palate is transversely arched. Its width between the first molars must have been about 45 mm., and it probably increased somewhat in width posteriorly. It is pierced by a foramen medially to M^1. The posterior border of the palate has not been preserved.

Comparisons. The infraorbital foramen is above the anterior part of M^1 in *C. rusingense*, *C. grande*, *C. brevirostris* and *Schizotherium priscum*, but in *C. pilgrimi*, probably due to the youth of the specimen, it is a little farther forward, above the posterior part of P^4. The height of the foramen on the face is least in *Schizotherium*, most in *C. grande* : the index, distance of foramen from teeth/molar length, is 25 in *S. priscum*, 29 in *C. pilgrimi*, 32 in *C. rusingense* and 43 in *C. grande*.

In *S. priscum* and *C. grande* the zygoma arises above the posterior end of M^2, as in *C. rusingense*, but in *C. brevirostris* it arises a little farther forward (mid M^2) ; in juvenile specimens, such as the holotype of *C. pilgrimi*, it reaches the level of the anterior end of M^2.

The length of the face is unknown in *Schizotherium* and in *C. grande*. It has almost certainly been shortened in *C. brevirostris*, for in this species it is much shorter than in *C. rusingense*. The anterior margin of the orbit in *C. brevirostris* is above the

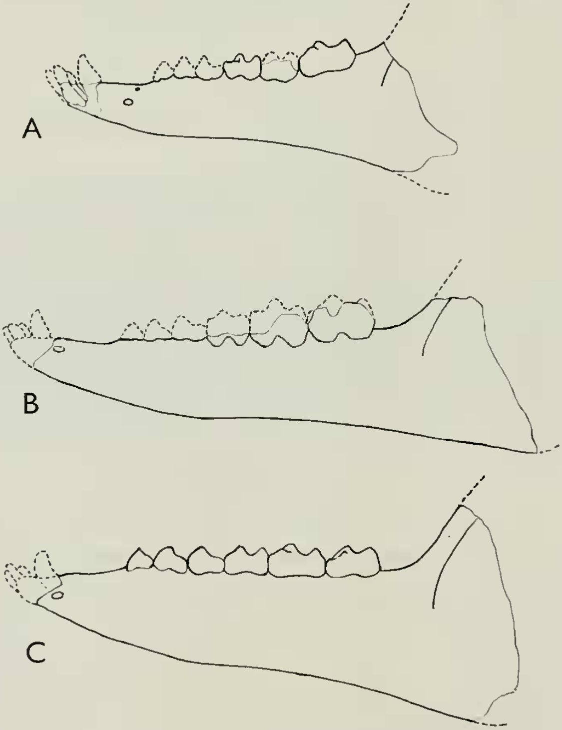

FIG. 8. Mandibles of *Chalicotherium*. A, *C. rusingense*, from Rusinga, F 3608. B, *C. wetzleri* (holotype of *Palaeotherium schinzii* von Meyer) from a cast. C, *C. grande*, Paris specimen from Sansan. All × ¼.

posterior part of M^2. Unfortunately the known skulls of *C. grande* are so badly crushed that the exact position of the border of the orbit is uncertain. The distance between the orbit and the infraorbital foramen appears, however, to be greater in *C. rusingense* than in either *C. grande* or *C. brevirostris*.

Mandible. (Text-figs. 8, 9 ; Table VII.)

F 3608 is the only specimen in which more than a fragment of the mandible is preserved. It consists of both horizontal rami, but the posterior part of the mandible has been broken off on both sides. R 283.48 shows the region of the symphysis.

The ramus is moderately deep, its depth increasing posteriorly. Below the molars the rounded lower border is very slightly concave in lateral view, falling and becoming sharper behind M_3 to indicate the angular process (most of which is missing). The lateral surface below the teeth is nearly flat, but shows a weak longitudinal groove about 14 mm. above the lower border. This groove fades out below the premolars, where there is a slight convexity. The masseteric fossa is very flat and hardly noticeable. The coronoid process appears to be inclined at an angle of 45° to the alveolar border. Internally, the ramus is moderately convex below the molars; about 15 mm. above the lower border there is a slight groove, presumably for the mylohyoid muscle. The mandibular foramen is low, its lower border being 22 mm. below the level of the alveolar border. The pterygoid fossa is very shallow.

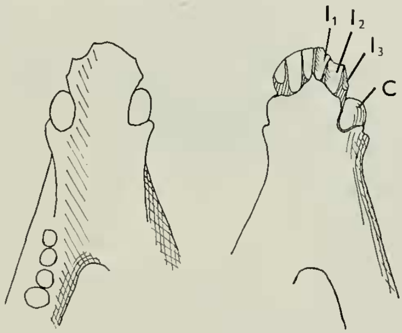

FIG. 9. *Chalicotherium rusingense*, F 3608, symphyseal part of mandible, in dorsal and ventral views, × ½.

The two rami converge at an angle of 30°. The symphysis extends back to the posterior end of P_2. The symphyseal region is nearly in line with the horizontal ramus, but shows a slight upward tilt. Its vertical depth is less than that of the ramus, and there is a step in the alveolar border anterior to P_2. The lower surface of the symphysis is evenly convex in a transverse direction, and its upper surface is concave to form a gutter. In the region of the diastema the alveolar border forms a sharp ridge, which turns laterally immediately behind the canine, where it overhangs the lateral surface of the jaw. The mental foramen is placed below the diastema, about midway between P_2 and the canine. Above it is a small foramen, close to the alveolar border.

Comparisons. *C. rusingense* resembles *C. grande* and *C. wetzleri* in the general shape of the horizontal ramus of the mandible. The anterior part of the mandible of *C. grande* is known mainly from a juvenile specimen figured by Filhol (1891, pl. 44). This differs from *C. rusingense* in the shorter symphysis and diastema. In an adult specimen (Filhol 1891, pl. 45) the diastema is only 58% as long as the premolar series, compared with 80% in *C. rusingense*, and it is probable that the anterior part of the mandible, and therefore also the tip of the snout, was more abbreviated in *C. grande* than in *C. rusingense*. A further difference is that the mandibular foramen of *C. grande* is in line with the teeth, whereas in *C. rusingense* it is at a lower level.

The mandible of *Schizotherium* is very poorly known. From the figure of Osborn (1912) it may be seen that the alveolar border is stepped down anteriorly to P_2 as in *Chalicotherium*. In *Schizotherium* sp. (Bohlin 1946) the symphysis ends a little anteriorly to P_2, and the diastema was evidently longer than in *C. rusingense*. In this specimen the coronoid process appears to rise rather steeply, resembling *Eomoropus* (Osborn 1913). In *S.* cf. *avitum* (Teilhard de Chardin 1926) the diastema is longer than the premolar series, and the symphysis ends far anterior to P_2, as in Eomoropinae. Shortening of the anterior part of the mandible appears to be a trend of chalicotherian evolution, and it is probable that *C. rusingense* is more primitive than *C. grande* in this respect.

TABLE VII.

Measurements of lower jaw, F3608.

Antemolar length (est.)	95 mm.
Between M_1 and the canine alveolus	63·5 mm.
Length of diastema	27·5 mm.
Length of symphysis (est.)	63 mm.
Length M_1–M_3 inclusive	70 mm.
Length P_2–P_4 inclusive	36 mm.
Depth at posterior end of M_3 (perpendicular to lower border)	49·5 mm.
Depth at anterior end of M_1	34 mm.
Depth at diastema	22 mm.
Width between canines	14 mm.
Minimum width behind canines	26 mm.
Width across M_3 talonids	92 mm.

Scaphoid. (Text-fig. 10 A–F.)

The only specimen of this bone is F 2077, which belongs to the left side. It is a proximodistally flattened bone with a distal (or "centrale") process, situated towards the ulnar and dorsal (= anterior) sides. Its dimensions are : height 31 mm., dorsovolar length 31 mm., radio-ulnar width 44·5 mm. In proximal view, the bone is transversely widened ; most of the proximal surface is occupied by the facet for the radius. This facet is concave in a dorsovolar direction ; its ulnar edge meets the proximal margin of the lunate facet in an acute angle, and its margin is slightly raised near the middle of the dorsal side and again at the ulnar end of the volar side. The radial third of the proximal surface of the scaphoid forms the radial process, and the middle of the volar side extends as a small volar process.

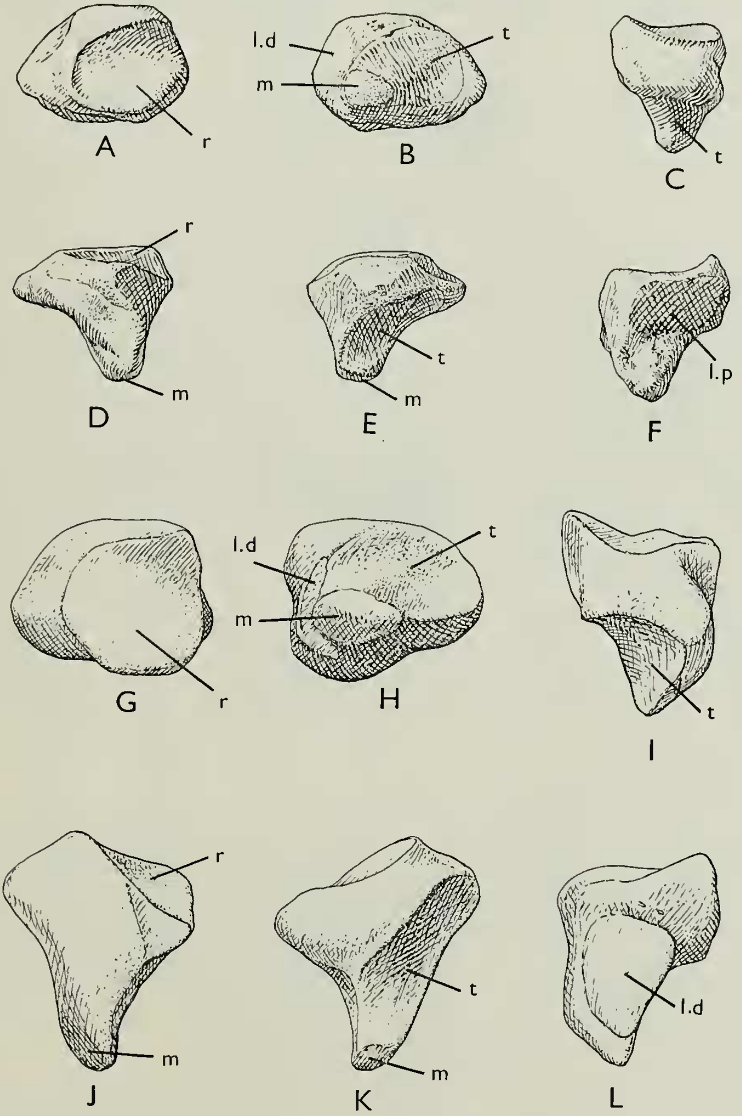

FIG. 10. A–F, left scaphoid of *Chalicotherium rusingense*, F 2077. A, proximal view ; B, distal view ; C, radial view ; D, dorsal view ; E, volar view ; F, ulnar view. G–L, corresponding views of scaphoid of *C. grande*, Paris specimen from Sansan. All × ½. Labelling of facets : *l.d.*, distal lunate ; *l.p.*, proximal lunate ; *m*, magnum ; *r*, radius ; *t*, trapezoid.

In dorsal view the scaphoid is wider than long. The dorsal surface is divided by a ridge which runs from the elevation in the dorsal margin of the radius facet to the distal process. This ridge divides a smooth, triangular proximo-ulnar area from the remainder, which is roughened. The roughening is very marked in a line from the radial process along the edge of the trapezoid facet, presumably for ligamentary attachment.

The trapezoid facet occupies a large area on the distal side of the bone, extending from the radial process to the radial side of the distal process. It is slightly saddle-shaped, being weakly divided by a ridge which arises from the tip of the distal process, near the dorsal side, and crosses the facet to end below the volar process. Radially, the trapezoid facet does not reach the tip of the radial process, but it leaves a small area of smooth bone that might have articulated with a trapezium.

On the ulnar face of the scaphoid there is a proximal facet for the lunate, but no distal lunate facet, the ulnar surface of the distal process being rough. The magnum probably articulated with a small convex area at the tip of the distal process.

Comparisons. The scaphoid of *Schizotherium* is unknown. In comparison with *C. grande*, of which four examples were studied in Paris, the scaphoid of *C. rusingense* appears to be compressed in a proximodistal direction. Its distal process is shorter and less slender. In *C. grande* the proximal lunate facet is hardly indicated, but there is a large distal lunate facet on the ulnar side of the distal process ; in *C. rusingense*, on the other hand, the proximal lunate facet is well developed, but the distal facet is absent. In *Phyllotillon betpakdalensis* (Borissiak 1946) and *Moropus elatus* (Holland & Peterson 1913) both facets are equally developed, and this is probably the primitive condition. The two species, *Chalicotherium grande* and *C. rusingense*, agree in the cylindrical concavity of the radius facet, which is saddle-shaped in *Phyllotillon* and flat in *Moropus*, and in the small and indistinct contact with the magnum, the distal process terminating in a rounded point, instead of being truncate as in the other genera.

Third Metacarpal. (Text-fig. 11 A–E.)

F 2070 is the proximal end of a right metacarpal III. The transverse diameter of its head slightly exceeds the dorsovolar diameter (37·5 × 35·5 mm.). The proximal surface is crossed by two dorsovolar keels, which demarcate the rectangular facet for the magnum. The ulnar keel is much the higher of the two. On its ulnar side is the unciform facet, and the radial part of the proximal surface is occupied by a facet for metacarpal II. The unciform facet extends onto the proximal surface of the prominent dorso-ulnar process, which overhangs a cavity on the ulnar side of the head of the metacarpal for articulation with metacarpal IV.

The facet for metacarpal II is triangular, tapering in a volar direction. It is convex in a dorsovolar direction ; its volar part is approximately horizontal and its dorsal part nearly vertical. The dorsoulnar part of the facet faces radially, extending onto the radial side of the keel that divides it from the magnum facet. The metacarpal facet overhangs the radial side of the bone. The magnum facet is also convex in a dorsovolar direction, but its dorsal part does not reach so far distally as

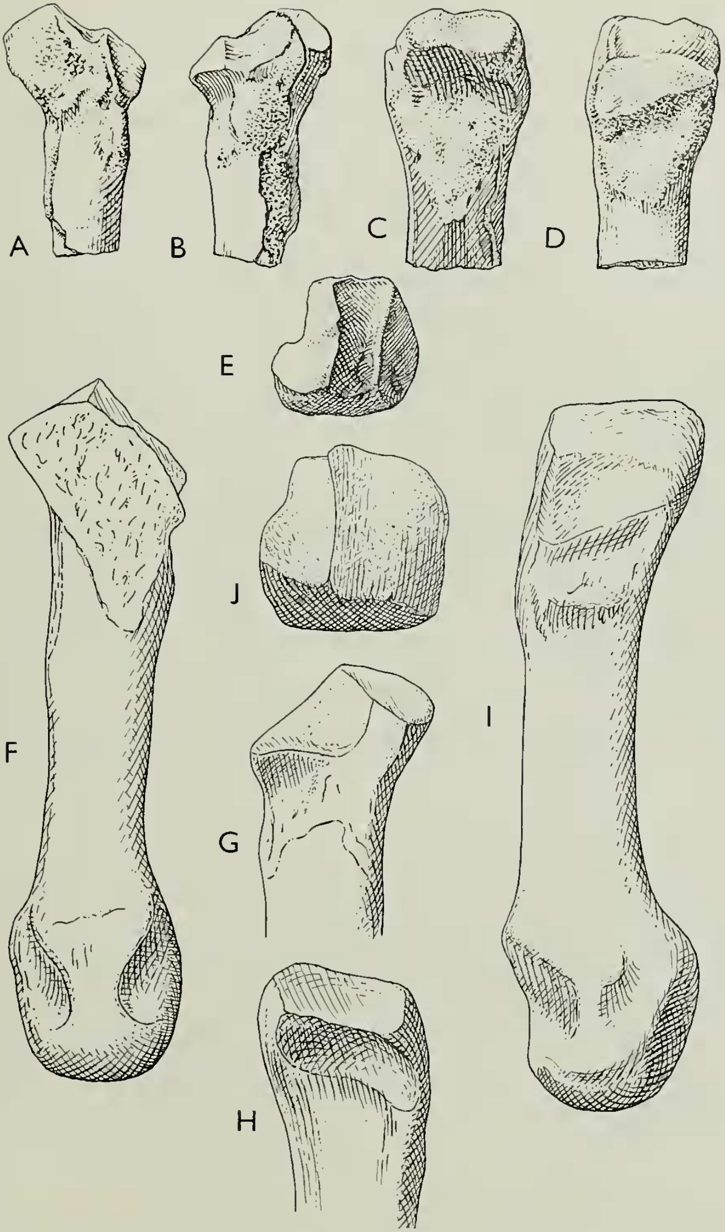

FIG. 11. A–E, right third metacarpal of *Chalicotherium rusingense*, F 2070. A, dorsal view ; B, volar view ; C, ulnar view ; D, radial view ; E, proximal view. F–J, corresponding views of *C. grande*, Paris specimen from Sansan. All × $\frac{1}{2}$.

the metacarpal facet, and it is bounded dorsally by a ridge. Transversely the magnum facet is concave, extending up its marginal keels. In the unciform facet, a dorsal part, which is concave, may be distinguished from a volar part, which faces in an ulnar direction. The dorsal part is situated on the dorso-ulnar process. A single facet for metacarpal IV occupies the proximal and radial sides of a pit on the ulnar side of the head ; its dorsal part faces in a distal and volar direction, and its volar part in an ulnar and somewhat distal direction.

The shaft is approximately quadilateral in section immediately below the head, but at the broken end, 67 mm. from the most proximal part of the head, the section is oval, somewhat flattened in a radio-ulnar direction. The surface of the bone near the head shows areas of roughening : on the dorsal surface of the dorso-ulnar process ; on the dorsal surface below the facet for metacarpal II, extending about 25 mm. distally ; on the radial side extending 18 mm. below the most distal part of the facet for metacarpal II ; on the volar side below the magnum facet, where the roughening forms a distinct prominence. The surface of the bone on the ulnar side is badly preserved.

Comparisons. The third metacarpal of *Schizotherium priscum* was figured by Filhol (1893) and described by Holland & Peterson (1913). A similar metacarpal from Mongolia, referred to *Schizotherium* sp., was figured by Colbert (1935). In both of these, the head of the metacarpal is smaller than in *C. rusingense* (cir. 25·5 × 27 mm. in Colbert's specimen). The radio-ulnar width of the head is less than the dorsovolar diameter, whereas in *C. rusingense*, and in *C. grande*, it is greater. The magnum facet occupies a larger proportion of the proximal end. The articulation with metacarpal II consists of two parts, a dorsal part, where the radial apophysis of metacarpal II projects over the proximodorsal surface of metacarpal III (as in *Moropus*), and a proximal part, which is narrower than in *C. rusingense* and is not separated from the magnum facet by a crest. The unciform facet is more steeply inclined and confined to the dorsal half of the bone (again as in *Moropus*). Colbert's specimen also resembles *Moropus* in bearing two facets for metacarpal IV.

In *C. grande* there is much more resemblance to *C. rusingense*. The differences noted are as follows : it is about one-third larger ; the keel separating the magnum facet from the facet for metacarpal II is weak or absent ; the magnum facet is less concave in a radio-ulnar direction. In other respects *C. grande* and *C. rusingense* resemble each other and differ from *Schizotherium* : the proportions of the head : the shape of the articulation for metacarpal II ; the extension of the unciform facet to the volar side of the head, and its more horizontal inclination ; the union of the facets for metacarpal IV.

Fourth metacarpal. (Text-fig. 12 A–E.)

There are two examples of the proximal end of metacarpal IV. The larger of the two, from site R 106, fits against the third metacarpal described above. It measures 36·5 mm. in dorsovolar length and 30 mm. in width. The other specimen (R278.55) is much smaller, (26·5 × 18·5 mm.) and probably juvenile.

In proximal view the larger specimen has the form of a triangle, flattened in a radio-ulnar direction. The most acute apex of the triangle is formed by the dorsal apophysis, which supports the dorsal part of an elongated facet for metacarpal III. The volar part of this facet is nearly vertical and faces radially. Most of the proximal surface is occupied by the unciform facet, which is triangular and nearly flat, but with its ulnar border somewhat elevated. It is separated from the volar part of the metacarpal facet by a blunt ridge, which however does not extend to the dorsal side. The head bears a small, truncated ulnar process, the surface of which is somewhat smoothed, perhaps representing a contact with a fifth metacarpal. Like metacarpal III, the surface immmediately distal to the head is very rugose, especially in a line from the dorsal apophysis to the ulnar process, and over an area extending 40 mm. down the volar surface.

In the juvenile specimen the dorsal apophysis is more weakly developed, and there is less rugosity. No facet for a fifth metacarpal can be distinguished.

Comparisons. Metacarpal IV of *Schizotherium priscum* has been figured by Filhol (1893), and that of *S. turgaicum* by Borissiak (1921) and Belyaeva (1954). In these, the head is less developed in a dorsovolar direction, owing to the absence of the dorsal apophysis. The facet for metacarpal III resembles that of *C. rusingense*, but faces more laterally, the uncinate facet occupying almost the whole of the proximal surface of the bone. There is a facet for metacarpal V on the ulnar side of the head.

In *C. grande* the dorsal apophysis is developed as in *C. rusingense*. The dorsal and volar parts of the facet for metacarpal III are not so clearly differentiated, and the ridge demarcating the unciform facet extends right across the head to the dorsal surface. Metacarpal V is absent, and the ulnar process is more prominent and less truncated than in *C. rusingense*.

Sesamoid.

F2079 is tentatively identified as a sesamoid of the manus of *C. rusingense*. It is a curved, flattened bone, trapezoidal in volar view. Its medial edge is straight, and bears a facet for articulation with the metacarpal keel. Its dorsal side is largely occupied by the cylindrically concave part of the joint surface. The lateral edge of its volar surface is raised to a ridge, forming the margin of the groove through which passes the main flexor tendon of the digit. The greatest length of the bone is 38 mm., the greatest width 19 mm.

Comparison. Although the sesamoids of chalicothere feet must have been comparatively large, they have been described only in the case of *Moropus elatus* (Holland & Peterson 1913). These differ from the specimen referred to *C. rusingense* in possessing a volar process for ligamentary attachment near the distal end, and in the frequent presence of a facet by which one sesamoid articulates with its partner.

Astragalus. (Text-fig. 13.)

The only example of this bone is MFW1208.55. It is not quite complete, part of the distal surface having been broken away.

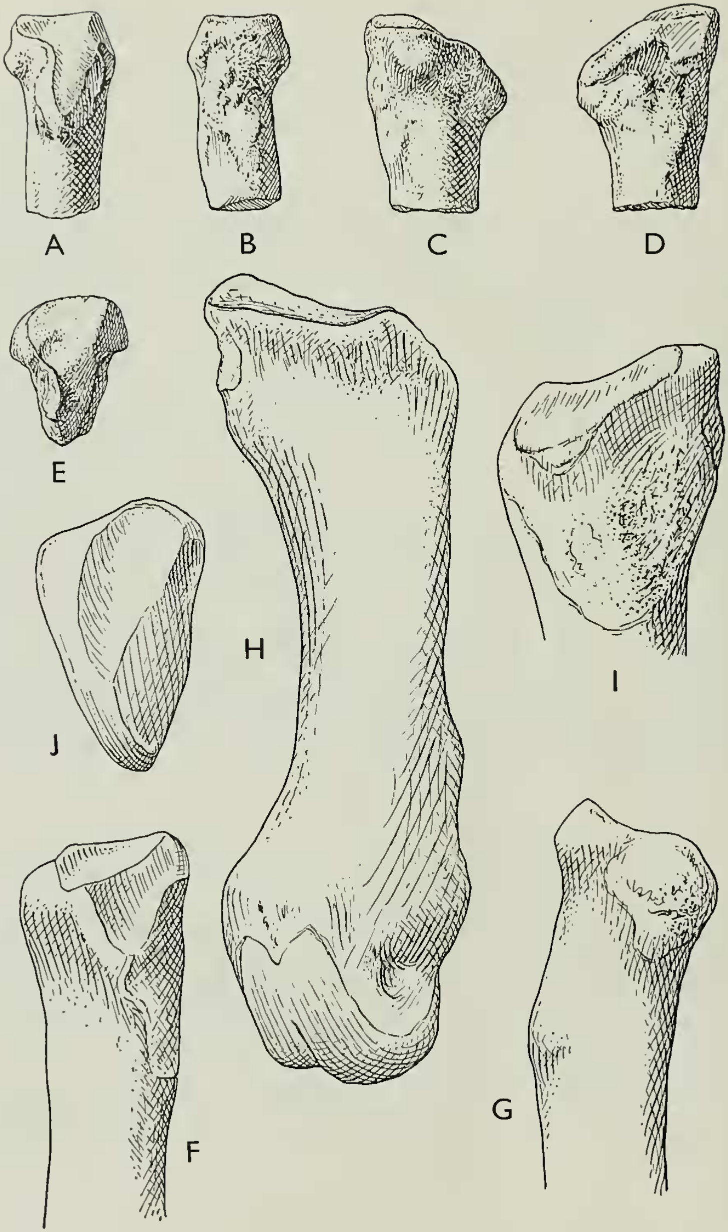

FIG. 12. A–E, right fourth metacarpal of *Chalicotherium rusingense*, from site R 106. A, dorsal view ; B, volar view ; C, ulnar view ; D, radial view ; E, proximal view. F–J, corresponding views of *C. grande*, Paris specimen from Sansan. All × ½.

In dorsal (=anterior) view the astragalus is much broader than high : its transverse diameter is 67 mm. and its height on the tibial side is 35·5 mm. The trochlea is correspondingly reduced in height, with the keels only moderately developed. Each keel subtends an angle of about 120°, but the fibular keel faces less proximally than the tibial keel ; in dorsal view it reaches farther proximally and distally. The neck of the astragalus, distally to the trochlea, is very short (about 5 mm. high).

In volar (=posterior) view may be seen a large, slightly concave, ectal facet on the fibular side, separated by a groove from the small, rounded, slightly convex sustentacular facet on the tibial side. The ectal facet extends more than half-way across the astragalus. Proximally it meets the trochlea in an acute edge, and distally on the fibular side it meets the small, flat distal calcaneal facet in a blunt angle. The sustentacular facet is separated proximally from the tibial part of the trochlea by a groove that leads to the astragalar foramina.

In distal view the fibular half of the astragalus is seen to be much narrower than the tibial half : the dorsovolar diameter at the fibular keel is 24 mm., and at the tibial keel it is 43 mm. Most of the distal surface is occupied by the navicular facet, which extends from the tibial border more than half-way across the bone. It is divided by a rounded convexity into two slightly concave areas, the larger one being dorsal, and the smaller one tibial and volar. Owing to breakage the presence of a cuboid facet cannot be determined ; it could not have been more than of limited extent.

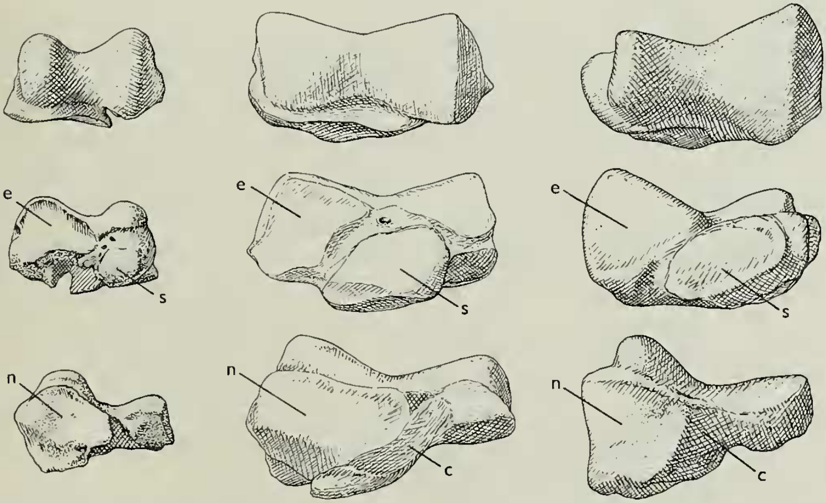

FIG. 13. Left astragali of *Chalicotherium*. Left, *C. rusingense*, MFW 1208.55, anterior (dorsal), posterior and distal views. Centre, corresponding views of *C. grande*, Paris specimen from Sansan. Right, corresponding views of *C. goldfussi*, from Pikermi, BMNH. M11351. All × $\frac{1}{3}$.
Key: *c*, cuboid facet ; *e*, ectal facet ; *n*, navicular facet ; *s*, sustentacular facet.

The tibial surface of the astragalus is much roughened, and near the trochlea it is marked by a deep pit for a ligament.

Comparisons. The astragalus of *Schizotherium turgaicum* (Borissiak 1946, Belyaeva 1954) is proportionately much higher than in *C. rusingense*, but the neck is equally short, the greater height being shown in the trochlea. The trochlear keels are more acute, and, on the volar side, the sustentacular and ectal facets are more elongated proximo-distally. In distal view the astragali of the two species are more similar, except that in *C. rusingense* the fibular part of the bone is narrower relatively to the tibial part. There is no cuboid facet in *S. turgaicum*.

In *C. grande* the astragalus is lower than in *C. rusingense*, and has blunter trochlear keels. The ectal facet is deeper, and does not extend so far towards the tibial side (see Wegner 1913). In distal view the fibular part of the astragalus is narrowed to the same extent as in *C. rusingense*. A cuboid contact is present in *C. grande* in the form of a strip along the posterior edge of the navicular facet (figured by Holland & Peterson 1913). The navicular facet is tilted towards the tibial side to a more marked degree in *C. grande* than in *C. rusingense*, and, probably associated with this, the tibial height of the astragalus is only 75% of the fibular height in *C. grande*, compared with 87% in *C. rusingense*.

Second Metatarsal. (Text-fig. 14 ; Table VIII.)

There are three examples of this bone. The best preserved is MFW1213.55. F2071, which is somewhat weathered, is similar but a little longer. Sgr82.48 is a small, juvenile specimen.

The proximal end is triangular in outline, with dorsal and volar processes, situated towards the fibular side, and a tibial process. Most of the proximal surface is occupied by the facet for the mesocuneiform, slightly concave in the tibio-fibular direction. On the fibular side of this is the facet for the ectocuneiform, which in MFW1213.55 is differentiated into dorsal and volar portions. The dorsal portion faces in a fibular direction, and is separated from the mesocuneiform facet by a sharp crest ; the volar portion faces proximally, and is separated from the mesocuneiform facet only by a low crest. In F2071 the dorsal portion is missing, perhaps due to weathering. There is no entocuneiform facet. On the fibular side, below the ectocuneiform facet, is an overhung facet for metatarsal III ; this apparently does not extend to the extreme volar side of the bone. Below it again is a roughening of the surface for ligamentary attachment. The dorsal process projects beyond the fibular side of the bone and extends for a short distance down the shaft.

The middle of the shaft is oval in section, somewhat flattened in a dorsovolar direction. The bone as a whole is short in comparison to its width : the total length is 2·0–2·1 times the maximum width of the distal end.

The distal articulating surface is placed obliquely to the long axis, its tibial side being more proximal than its fibular side. In F2071 its dorsal border is separated from the shaft by a shallow groove, but this is not present in MFW1213.55. Dorsally, the articulating surface projects beyond the level of the shaft, and forms a smoothly convex area for the phalanx. The volar part of the articulation, for

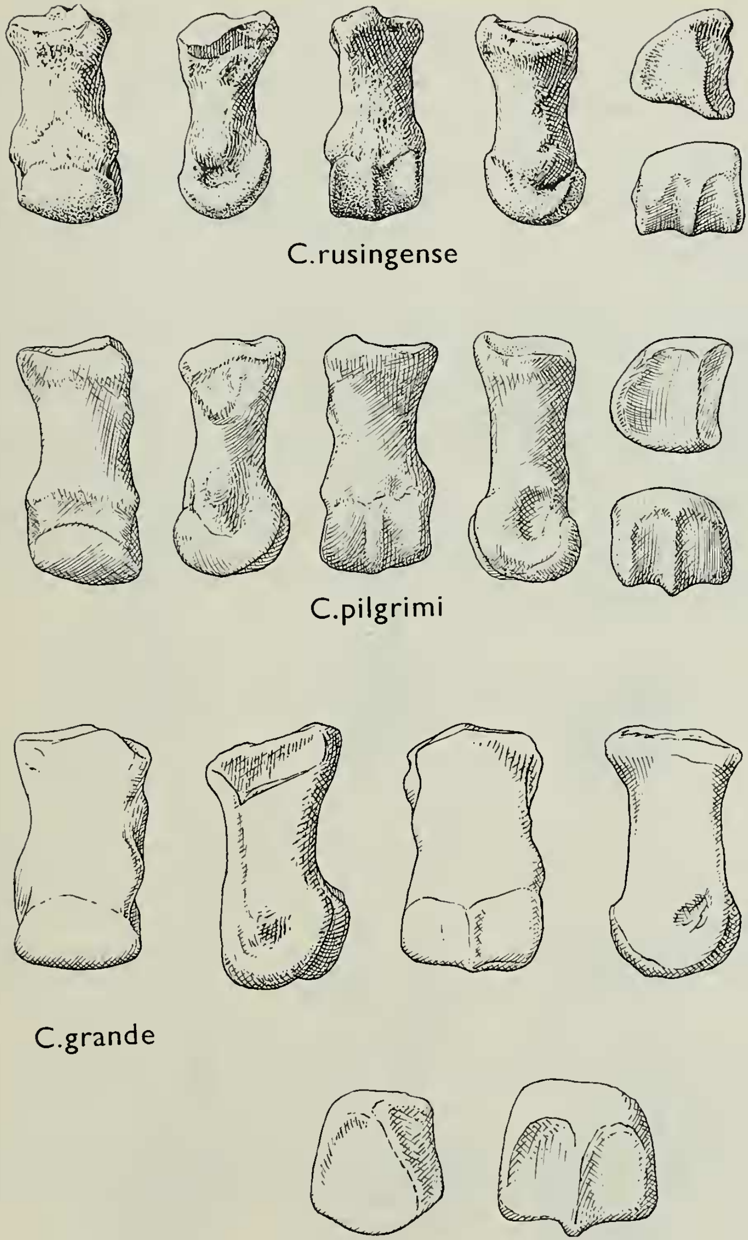

FIG. 14. Right second metatarsals of *Chalicotherium*. *C. rusingense*, MFW 1213.55, in dorsal, ulnar, volar, radial, proximal and distal views. *C. pilgrimi*, BMNH. M12168, corresponding views. *C. grande*, Paris specimen from Sansan, corresponding views. All × ½.

the sesamoids, is divided by a median keel which starts at the most distal end of the bone. The groove on the tibial side of this keel is more deeply cut than the groove on the fibular side. Proximally to the distal articulation, apophyses for ligaments are developed on the lateral sides of the bone ; below each, but most marked on the fibular side, is a pit.

Comparisons. In *Schizotherium priscum* (Filhol 1893) and *S. turgaicum* (Borissiak 1921) the second metatarsal is much more elongated (length/distal width 4·0 and 4·3 respectively, cf. 2·0–2·1 in *C. rusingense*). In *C. pilgrimi* (BM.12168) it is shortened to the same degree as in *C. rusingense* (2·1) but in *C. grande* it is somewhat shorter (1·7–1·9).

In proximal view the head is more compressed in a tibio-fibular direction in *Schizotherium* than in *Chalicotherium*. *C. pilgrimi* is very much like *C. rusingense* in the shape of the proximal end, but in *C. grande* the head is trapezoidal rather than triangular, owing to broadening on the volar side.

In *S. turgaicum* the ectocuneiform facet is divided into two. In the species of *Chalicotherium* it is single, but *C. rusingense* and *C. pilgrimi* show more clearly than *C. grande* a functional division between a more vertical dorsal part and a more proximal volar part. In *C. grande* the crest separating the ectocuneiform and mesocuneiform facets is blunt throughout its length, whereas in *C. rusingense* and *C. pilgrimi* its dorsal half is acute.

TABLE VIII.

Measurements (mm.) of metatarsals of *C. rusingense*.

	Second			Third			
	MFW 1213·55	F2071	Sgr. 84·48	F2076	R30	R648·47	R91
Width of head	27	26	21·5	25	23·5	17·5	23
Dorso-volar, head	28	24·5	20	28	30·5	24	25
Minimum width, shaft	20·5	23·5	15·5	23	22·5	15·5	19
Distal width, across articulation	28	29	21	26·5	27	21·5	24
Length	58	58·5	50	69	62·5	58	57·5

The overhung facet for metatarsal III is double in *S. turgaicum*, single in the three species of *Chalicotherium*.

At the middle of its length the shaft is more nearly circular in cross-section in *Schizotherium* than in *Chalicotherium* where it is somewhat broadened. In *C. grande* the shaft is broader in comparison with the distal width than in *C. rusingense* or *C. pilgrimi*.

Third metatarsal. (Text-fig. 15 ; Table VIII.)

Four specimens are identified as this bone, although they differ somewhat in size and proportions. The longest specimen is F2076 (left). Another specimen (left) from R30 is of the same width but slightly shorter. R648.47 (left) and a specimen from R91 (right) are smaller and more slender, and may be juvenile.

The ratio of length/distal width ranges from 2·2 to 2·6, and it is probable that metatarsal III was slightly longer than metatarsal II of the same individual, though of similar width. There is some variation in the shape of the section of the middle of the shaft : thus in F2076 the transverse diameter slightly exceeds the dorsovolar diameter, but in R648.47 the dorsovolar diameter is the greater, while the specimen from R30 is nearly circular in section.

The proximal surface is roughly triangular or trapezoidal. It is inclined distally towards the dorso-fibular apex, and is occupied by a very slightly convex facet for the ectocuneiform. There is no distinct facet for the cuboid. The fibular edge, which is nearly perpendicular to the straight dorsal edge, is slightly concave in F2076, straight in the other specimens. The third edge, from the tibio-dorsal apex to the fibulovolar apex, is convex. In all specimens the dorsovolar diameter of the head is greater than the transverse diameter, but less markedly so in the specimen from R91 than in the others.

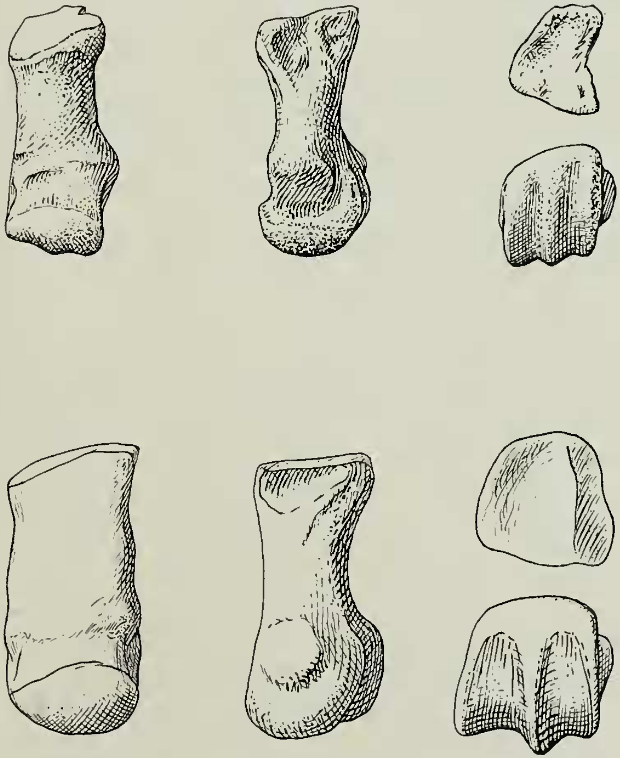

FIG. 15. Right third metatarsals of *Chalicotherium*. Above, *C. rusingense*, F 2076, in dorsal, ulnar, proximal and distal views. Below, *C. grande*, Paris specimen from Sansan, corresponding views. All × $\frac{1}{2}$.

On the most proximal part of the fibular surface of the metatarsal are two facets for articulation with metatarsal IV, slightly overhung by the fibular border of the proximal surface. Each facet occupies the proximal part of a pit in the fibular surface. The more dorsal facet is the larger ; it is somewhat concave, and faces slightly in a volar direction. The volar facet is smaller and flatter.

The distal end is tilted towards the tibial side to a greater extent than in metatarsal II. The fibular ligamentary apophysis is much better developed than its tibial counterpart, whereas on metatarsal II they are more equal. The dorsovolar diameter of the distal end is relatively greater than in metatarsal II, exceeding the transverse diameter. The sesamoid articulation is accordingly more extensive than the phalangeal articulation. The fibular sesamoid groove is more deeply incised than on metatarsal II, though it remains shallower than the tibial groove.

Comparisons. This metatarsal is much shorter in comparison with its width than in *Schizotherium priscum* (Filhol 1893) and *S. turgaicum* (Borissiak 1921). It is much more like *C. grande*, though only the specimen from R30 agrees with that species in proportions, the other specimens being relatively longer.

In *Schizotherium* metatarsal II is much more slender than metatarsal III, but in *C. grande* the two metatarsals are of equal width, and this appears to be so also in *C. rusingense*.

C. rusingense resembles *Schizotherium* in the proportions of the proximal end of the bone ; in *C. grande* it is rather broader. In *C. grande* there is a distinct cuboid facet, absent in *C. rusingense* and in *Schizotherium*. *C. rusingense* also agrees with *Schizotherium* in the possession of two distinct facets for metatarsal IV ; in *C. grande* the volar facet is apparently absent.

The distal ends of metatarsals II and III of *C. grande* differ in the same ways as those of *C. rusingense*, but the differences are less marked.

Basal phalanges. (Table IX.)

Of 43 basal phalanges, 23 are referred to the manus, because of their larger size and their resemblance to phalanges of the manus of *C. grande*. The 23 specimens fall into three groups, regarded as representing digits II, III and IV.

Digit II of manus. (Text-fig. 16A). This type of phalanx is so identified from its resemblance to the basal phalanx of B.M. M8638, a complete digit of *C. grande*, including the metacarpal. It is broader proximally than distally. The proximal border forms two lobes of which the radial is the more prominent. The facet for the metacarpal occupies the proximal half of the dorsal surface of the bone. It is concave, and faces very slightly proximally and radially. Its ulnar border is marked by a prominent crest which reaches its greatest height at the disto-ulnar extremity of the facet. Its radial border is lower, broadening out distally to form a crescent-shaped flattened area that possibly marks the insertion of an extensor tendon. Distally to the metacarpal facet the phalanx narrows to a waist, especially conspicuous in lateral view. On the volar side there is a broad longitudinal concavity between two marginal ridges. Each of these ridges is developed into a proximal prominence, and about half-way along the bone there is a second, smaller prominence

TABLE IX.

Measurements (mm.) of some phalanges, *C. rusingense.*

Basal phalanges	Manus II		Manus III		Manus IV		Pes	
	R450.47	R136a.49	R189.47	R945.47	R136.49	F2074	MFW 1214.55	R452.47
Ulnar length	56·5	49·3	60·2	57	63	56·2	42·4	39
Radial length	59	50	58·3	54·5	59·7	51·2	40·2	36·5
Length of metapodial articulation	25·7	20·8	25·2	21·5	27·5	25·7	21	20·2
Length distal to metapodial articulation	22	20·5	23·1	23·3	24	19·7	15	13·5
Proximal width	34	31	36·5	33	39·5	33·5	30·5	27·4
Distal width	23	22·5	25·1	22·3	27	24·2	23	19·8
Thickness	25·5	23·6	26·7	22·9	26·5	23·2	19·5	19·4

Middle phalanges	Manus			Pes		
	R136b.49	R757.47	R748.50	MFW 1217.55	R233.51	R844.48
Maximum length	45	39	38	30	28	25·5
Proximal width	27·5	21	24	21·5	18·5	18·5
Width across trochlea . . .	22	15·5	19	18·5	15·5	14
Height of trochlea. . . .	37	28	30	24	22	21·5

Ungual phalanges	Manus		Pes	
	R136c.49	R134.49	R160.49	R922.47
Maximum length	96	—	—	64e
Length of base	66	60	48	41
Height of articulation . . .	30	26e	23	21
Height at cleft	44	43	40	32
Width of base	25	20·5	25	20
Width of articulation . . .	22·5	18	19	16

(intermediate volar tubercle). Distally, the marginal ridges merge into the keels that form the edges of the articulation for the middle phalanx. This articulation, which occupies the distovolar part of the bone, is in principle a trochlea, with median groove and lateral keels. However, it usually shows an incomplete subdivision into a distal part and a volar part. The bottom of the groove in passing from one part to the other forms a slight but distinct angulation ; the lateral keels diverge in the distal part, but are parallel in the volar part ; the joint surfaces on the sides of the groove, instead of being evenly curved, are incompletely differentiated into two areas corresponding to the two parts of the groove and keels. The articulation is not symmetrically placed in relation to the phalanx as a whole, but is arranged

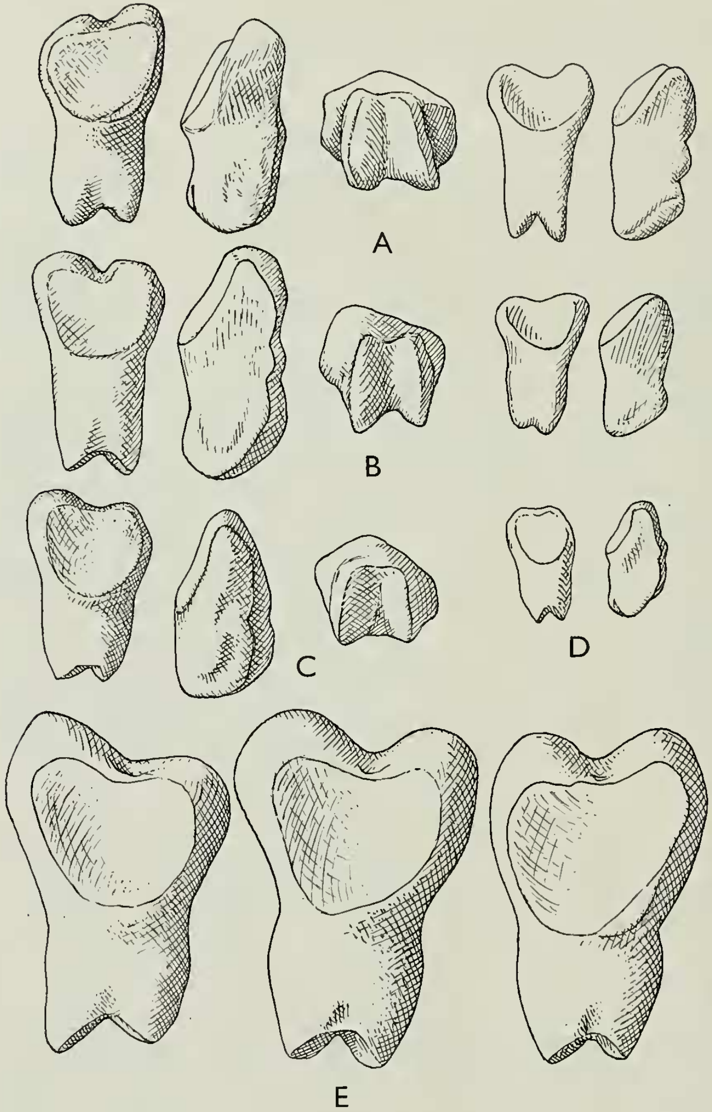

Fig. 16. Basal phalanges. A–C, *Chalicotherium rusingense*. A, R 450.47 (left manus), dorsal, radial and distal views. B, unnumbered specimen from site Rs 91 (right manus, reversed), dorsal, radial and distal views. C, unnumbered specimen from site Rs 30 (left manus), dorsal and radial views, and F 2075 (right manus, reversed), distal view. D, *Schizotherium priscum*, three phalanges from Paris Museum, dorsal and lateral views. E, *C. grande*, three types of basal phalanx of the manus, Paris Museum, in dorsal view. All × $\frac{1}{2}$.

so that its most dorsal end is displaced towards the ulnar side and its volar end towards the radial side. The lateral surfaces of the phalanx are marked by proximal and distal roughenings for ligaments. The ulnar surface is deeper and flatter than the radial surface, which is more convex and less distinctly marked off from the dorsal surface.

There are 8 examples of this bone, ranging in ulnar length from 44·3 to 56·5 mm. (mean 50·4), in radial length from 44·3 to 59 mm. (mean 52·4).

Digit III of manus. (Text-fig. 16B.) This phalanx averages rather longer and narrower than that of digit II. The metacarpal facet occupies less than half the dorsal surface ; the shaft distal to this facet is relatively longer and narrower, and the distal trochlea is also relatively narrower. The flattened area on the radial edge of the metacarpal facet is less conspicuous. The lobes of the proximal end are more equal, the ulnar lobe exceeding the radial lobe slightly. The intermediate volar tubercles are distal to the metacarpal facet.

Seven complete specimens range in ulnar length from 50·2 to 60·2 mm. (mean 57·3). There is also a larger specimen of which the ulnar length must have been about 68 mm.

This phalanx is identified as belonging to the third digit because it is the longest and most symmetrical of the three types.

Digit IV of manus. (Text-fig. 16C.) In this type the ulnar lobe of the proximal border is much more prominent than the radial lobe. It is shorter than the phalanx of digit III, and resembles that of digit II in length. The metacarpal facet occupies rather more than half the dorsal length, and the intermediate volar tubercles are placed opposite the distal part of the facet, as in digit II. This phalanx differs from that of digit II in being more stoutly constructed, in lacking a waist, and in the lack of a conspicuous area of flattening on the radial margin of the metacarpal facet, as well as in the different shape of the proximal border.

There are 7 examples of this bone, ranging in ulnar length from 46·5 to 65 mm. (mean 55·5).

Pes. (Text-fig. 17A–C.) The basal phalanges of the pes are smaller than those of the manus (ulnar length of 10 complete specimens, 37–44·3 mm., mean 40·8). The metatarsal facet faces more dorsally, and always occupies more than half of the dorsal surface. Intermediate volar tubercles are usually absent. The phalanges of the three digits of the pes appear to differ in much the same way as those of the manus, but to a smaller degree.

Two specimens, one from Rusinga (unnumbered) and one from Songhor (Sgr 32·47), though small (ulnar length 35·7 and 35·3 mm. respectively) are more slender than specimens referred to the pes. They are probably juvenile specimens from the manus.

Comparisons. The basal phalanges of the manus of *C. grande* are from one-third to one-half larger than those of *C. rusingense*. There are some differences in proportions : the proximal width is relatively greater, and the metacarpal facet occupies a greater proportion of the dorsal surface than in most specimens of

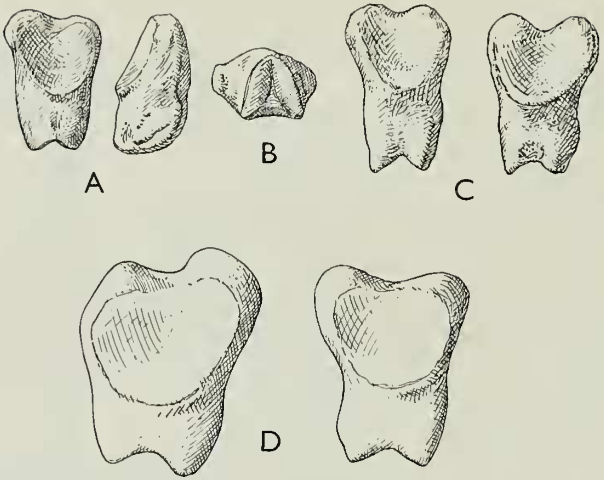

Fig. 17. Basal phalanges of the pes. A–C, *Chalicotherium rusingense*. A, R 452.47. B, R 281.51. C, Rusinga, no data. D, two phalanges of *C. grande*, Paris Museum. All × ½.

C. rusingense. The intermediate volar tubercles are very weakly developed. As in *C. rusingense*, phalanges of the pes are much smaller than those of the manus.

The phalanges of the manus of *C. grande* fall into three groups, presumably corresponding to the three digits, as in *C. rusingense.* (Text-fig. 16E.) The differences between them are not so great, however ; for example, phalanges referred to digit III are less obviously elongated, in comparison with those of digits II and IV, than in *C. rusingense.* Unfortunately, the articulated left manus described and figured by Gervais (1877) and by Holland & Peterson (1913) cannot be used to identify the phalanges of the different digits, for the digits appear to have been reconstituted artificially : the basal phalanx of digit IV belongs more probably to digit III of the right side ; that of digit II seems to belong to digit IV, and that of digit III to digit II.

Two basal phalanges may tentatively be referred to *C. pilgrimi* : B.M. 12170 and 12172 (Forster-Cooper 1920). From its symmetry, 12172 may be interpreted as from digit III of the manus. It is a little shorter than most specimens of *C. rusingense* of this type, agreeing in length more with those of digits II and IV. It is broader than any of the phalanges of *C. rusingense.* Its metacarpal facet occupies rather more than half of the dorsal surface, as in *C. grande.* Intermediate volar tubercles are well-developed. 12170 appears to belong to digit II, as the metacarpal facet extends more proximally on the radial side than on the ulnar side. It is somewhat larger than in *C. rusingense*, and its metacarpal facet is more extensive.

A phalanx of the pes, referred to *C. wetzleri* by Viret (1929) is very similar in size and shape to specimens of *C. rusingense.* It has an intermediate volar tubercle, like some of these.

Several basal phalanges of *Schizotherium turgaicum* are figured by Belyaeva (1953, pl. 3), and five specimens of *S. priscum* were examined in Paris (Text-fig. 16D). In each species the phalanges show a variety of size and form, but they cannot be allocated to the different digits on the same basis as in *Chalicotherium*. Filhol's (1893) drawings of the metapodials of *S. priscum* indicate that the phalanges of the pes are probably larger than those of the manus, at least on digits III and IV, as in *Grangeria* (Colbert 1934) : the largest phalanx in Paris is about as wide as the distal end of the third metatarsal. Most specimens resemble in general proportions those of digit III of the manus of *C. rusingense*, but they may be distinguished by the much more proximal orientation of the metacarpal (metatarsal) facet, which occupies less than one-third of the dorsal surface. In side view the distal trochlear keels are less convex, permitting less rotation of the middle phalanx. Intermediate volar tubercles are frequently present, as in *C. rusingense*. In a few specimens (one of *S. priscum* and two of *S. turgaicum*) the metacarpal facet faces more dorsally and occupies nearly half the dorsal surface, as in *C. rusingense*. In *Moropus* and *Phyllotillon* a similar dorsal orientation of the facet distinguishes the basal phalanx of digit II of the manus, and this may well have been true also of *Schizotherium*.

Middle Phalanges. (Text-fig. 18 ; Table IX.)

There are 28 middle phalanges in the collection. They vary in size : the larger ones probably belong to the manus and the smaller ones to the pes. The small

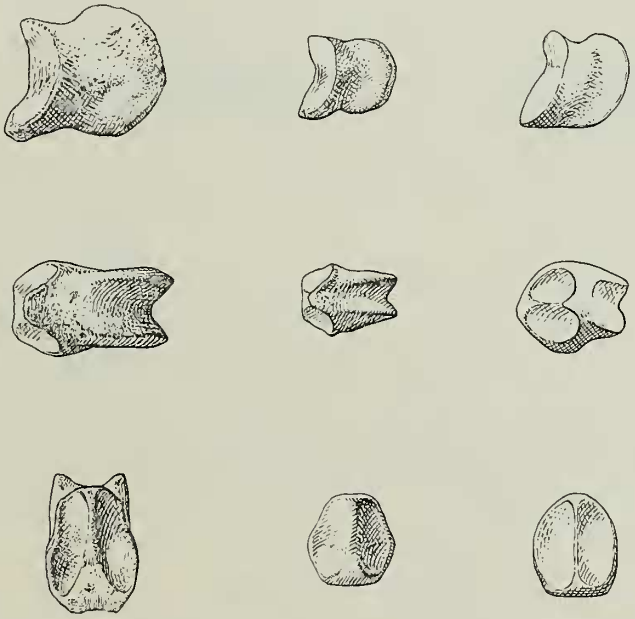

FIG. 18. Middle phalanges. Left, *Chalicotherium rusingense*, R 136.49, in lateral, dorsal and proximal views. Centre, *C. rusingense*, from site Rs 38. Right, *Schizotherium priscum*, Paris Museum. All × ½.

specimens, making up about half of the series, are more alike in size and shape than the large specimens, and it appears that the middle phalanges of the different digits of the manus are less uniform than those of the pes. The most compressed specimens, with narrow proximal and distal joint surfaces, probably belong to digit III of the manus, and the small phalanges, supposedly from the pes, are comparatively broad in relation to their length and height.

The phalanges are short, laterally compressed bones. The proximal surface is occupied by the articulation for the basal phalanx. This consists of a pair of lateral concave joint surfaces separated by a median keel. The keel runs from a pointed dorsal process, which in many specimens projects beyond the general dorsal surface of the phalanx, to a broader, truncated or slightly emarginate volar process. The volar part of the keel broadens out, the volar parts of the articulatory facets diverging from each other. The dorsal and volar parts of the keel often meet in a more or less distinct angle, corresponding to the angle in the groove of the distal articulation of the basal phalanx. In some specimens the lateral joint surfaces also show signs of a division into a dorsal part, facing proximally, and a volar part, facing more dorsally. The articulation for the basal phalanx is not symmetrically placed in relation to the median plane of the bone, but faces slightly towards the ulnar (fibular) side. The distal end of the phalanx is occupied by the articulation for the ungual phalanx. It has the form of a trochlea, consisting of a median groove and prominent lateral keels, semicircular in lateral view. Dorsally the keels are parallel, but towards the volar side they diverge slightly and the groove between them becomes shallower. The lateral surfaces of the phalanx are flattened, except at the distal margin of the proximal articulation, which projects laterally ; near the middle of each lateral surface is a pit for ligamentary attachment.

Comparisons. Except for their larger size, the middle phalanges of *C. grande* are indistinguishable from those of *C. rusingense.* In *C. grande* the phalanges of the pes are smaller and proportionately broader than those of the manus, as was postulated for *C. rusingense.*

A middle phalanx of *Schizotherium priscum* in Paris fits the larger basal phalanges. It compares in size with some phalanges of the manus of *C. rusingense,* but is relatively broader. Some middle phalanges of *S. turgaicum* described by Belyaeva (1954) are smaller than any of *C. rusingense,* and relatively broader. In the Paris specimen, the proximal articulation as a whole faces more dorsally than in *C. rusingense,* the volar part being more extensive and the dorsal part reduced. The distal trochlea faces more ventrally, its keels are more widely separated at their dorsal ends, and the groove between them is much shallower. *S. turgaicum* appears to possess the same characters. The middle phalanges of *Schizotherium* thus approach those of *Phyllotillon* and *Moropus.*

Ungual phalanges. (Text-fig. 19 ; Table IX.)

Seventeen ungual phalanges in the collection all have a similar structure, though they differ in size and proportions.

The phalanx is approximately triangular in side view, with a curved dorsal border which extends proximally to form a prominent dorsal process (preserved intact only in R136.42, and almost complete in R922.47). The articulation for the middle phalanx occupies most of the proximal surface and extends along the lower side of the dorsal process. It is curved in an arc of about 100°, and consists of a pair of elongated joint facets separated by a median keel. Below the articulation is a median pit, probably for the flexor ligament, and on either side of this a foramen through which blood vessels passed to the bed of the claw. The terminal part of the phalanx is split by a deep cleft, extending back more than halfway along the volar and dorsal surfaces. The volar surface proximally to the cleft is swollen into a rounded boss. The lateral surfaces of the phalanx are flattened and rather rugose. The bone is not quite symmetrical : in relation to the plane of the cleft the dorsal process is directed slightly towards the ulnar (fibular) side. The articulation is also asymmetrically arranged : its dorsal end (on the dorsal process) is ulnar (fibular) to its volar end. The volar boss is displaced a little towards the ulnar (fibular) side.

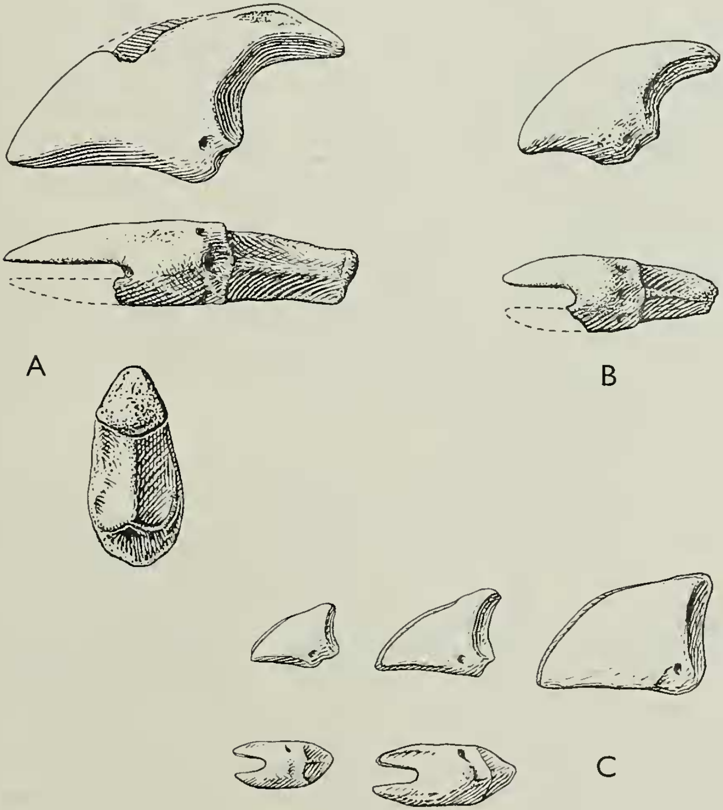

FIG. 19. Ungual phalanges. A, *Chalicotherium rusingense*, R 136.49, lateral, volar and proximal views. B, *C. rusingense*, R 922.47, lateral and volar views. C, Three phalanges of *Schizotherium priscum*, Paris Museum. All × ½.

The phalanges fall into two groups, which are probably to be referred to the manus and pes. Those of the pes are broader in proportion to length and height, and are more deeply cut by the claw cleft, the dorsal limit of this being perpendicularly above the volar boss. The distinction is particularly clear in the region of the volar boss : in the manus the horizontal length of the boss, measured from the end of the claw cleft, is about the same as the width of the phalanx (index 80–105) : in the pes it averages a little more than half the width (index, 47–70). The phalanges of the manus are on the average higher than those of the pes (height at volar boss : manus 38–52 mm., pes 32–42 mm.), and also longer in volar length (manus 50–66 mm., pes 41–52 mm.), but the ranges of width are similar. The radius of curvature of the proximal articulation is greater in the manus than in the pes. It has not been possible to allocate phalanges to individual digits with any certainty. It is likely that the largest phalanges belonged to digit II of the manus (e.g. R736.50 and R136.42) and pes (e.g. R497.42), but the preponderance of the claw on this digit of the manus was certainly much less than in *Moropus*.

Comparisons. There are four specimens of ungual phalanges of *Schizotherium priscum* in Paris, including a large specimen which compares in measurements with *Ancylotherium gaudryi* Filhol (1880). They are all rather broad, comparing in length/width relations with the phalanges of the pes of *C. rusingense*. Their height/width indices are, however, much less than in any specimen of *C. rusingense*, and there are various differences in detail : the dorsal process is less developed ; the proximal articulation has a less prominent median keel, and its curvature is less ; the volar surface is flattened and is separated from the lateral surfaces by sharp edges. An ungual phalanx of *S. turgaicum* figured by Belyaeva (1954) shows similar characters, but is even lower and broader. The largest specimen of *S. priscum* approximates in size to the smallest specimens of *C. rusingense*.

The ungual phalanges of *C. grande* are so similar to those of *C. rusingense* that it is possible to distinguish them only by size.

The Digit as a Whole. (Text-fig. 20.)

The second metatarsal MFW1214.55 fits the basal phalanx MFW1213.55 so well that they probably belong to the same individual. A satisfactory, but not perfect fit was found between the third metatarsal from R91 and the basal phalanx F2082. When the basal phalanx was placed so that the dorsal border of its articulating facet coincided with the dorsal border of the facet on the metatarsal, the angle between the dorsal surfaces of the two bones was about 72°. As in other chalicotheres therefore, the basal phalanx is capable of considerable hyperextension.

In this position, no appreciable rotation of the phalanx is possible round its own axis, but lateral sliding would result in some abduction or adduction of the digits. There is no evidence of the notches noticed by Matthew (1929) on the margin of the metacarpal facet of the basal phalanx of digit II in *Moropus*, and interpreted by him to imply two alternative positions of the digit. It is possible however that his " lateral notch " corresponds to the flattened area on the radial margin of the facet in *C. rusingense*, interpreted here as the insertion of an extensor ligament.

In maximum flexion the dorsal angle between the phalanx and the metatarsal opens out to no more than about 110°. Rotation beyond this point is prevented by the median keel on the metatarsal, which meets the notch in the proximal border of the phalanx. Presumably the more posterior part of the metatarsal joint surface was occupied by the sesamoid bones, which would remain in contact with the proximal end of the phalanx throughout the movement, being tied to it by a ligament, equivalent to the middle sesamoidal ligament of the horse.

Although the distal ends of the metacarpals of *C. rusingense* are not known, the similarity of the basal phalanges of the manus to those of the pes is such that considerations based on the pes may be taken to apply also to the manus. This is certainly true of *C. grande.*

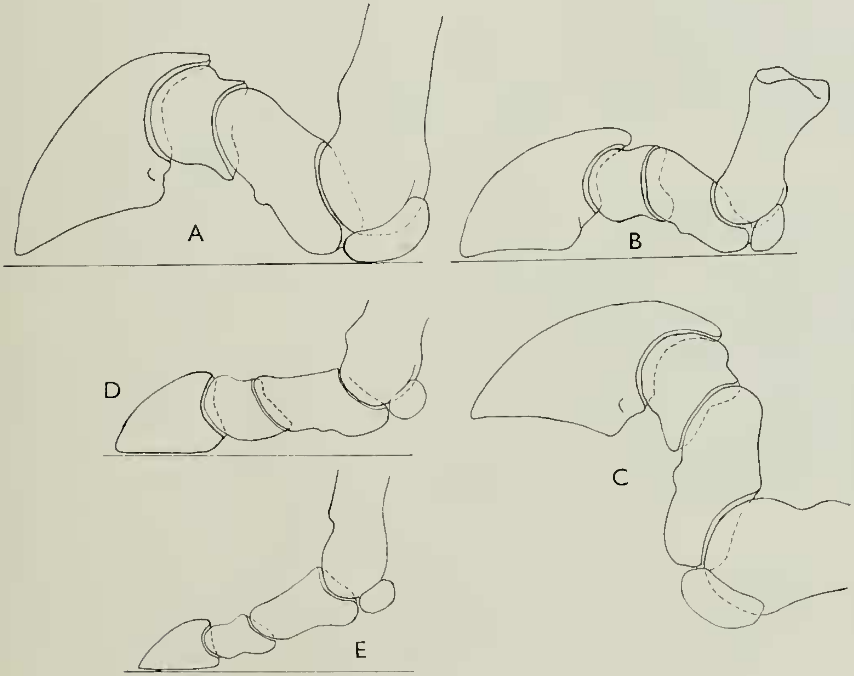

FIG. 20. Reconstructed toes. A–C, *Chalicotherium rusingense.* A, from the manus, walking position ; B, from the pes, walking position ; C, from the manus, clinging position. D, *Schizotherium priscum,* walking position. E, *Plagiolophus annectens,* walking position.

The joint between the basal and middle phalanges shows a partial differentiation into dorsal and volar portions, representing the areas of greatest pressure during extension and flexion respectively. By fitting phalanges together it may be seen that even in maximum extension the middle phalanx turns down on the basal phalanx ; the median axis of the middle phalanx makes an angle of 10–15° with the long axis of the basal phalanx. The rotation from maximum extension to maximum flexion is 30–40°, so that at maximum flexion the angle between the two phalanges is about 45°.

Movement between the middle phalanx and the ungual phalanx is greater : the angle of rotation appears to be about 60°. In maximum extension, the volar surface of the ungual phalanx lies approximately parallel to the median horizontal plane of the middle phalanx, but at a lower level, leaving space beneath the middle phalanx for the flexor tendon. The total amount of bending in the digit itself would be rather more than a right angle, to which must be added 40° or so at the metapodial-phalangeal joint.

When walking, the weight must have been received on the proximal ends of the basal phalanges, and presumably also on the sesamoids ; it is likely that a plantar pad existed in this region. The toes themselves did not play any part in supporting the animal. Reconstruction of complete digits shows that the claw probably rested on the ground, the toe being extended but forming an arch. By extreme extension the claw could be raised a little, which would be necessary when the animal was walking over rough ground. This is a much less specialized condition than that found in *Ancylotherium pentelicum* by Schaub (1943), in which the toes were held back against the dorsal sides of the metacarpals. Maximum hyperextension of the digit in *C. rusingense* would seem to be accounted for by pressure of the claw against the ground, aided by the main extensor ligament attached to the dorsal process of the ungual phalanx, but in *Ancylotherium* Schaub found it necessary to postulate the existence of elastic ligaments.

In *Schizotherium* the position of the proximal articulating surface of the basal phalanx shows that the degree of hyperextension must have been much less than in *Chalicotherium* ; it is doubtful whether the distal end of the phalanx could be raised above the proximal end. The known middle and ungual phalanges appear to indicate a digit that was straight, inclined downwards at a small angle, and placed so that the flattened volar surface of the ungual phalanx rested on the ground. The elevation of the proximal part of the basal phalanx above the ground seems to have been small, and much of the weight of the animal might well have been supported by a pad at the base of the digit ; nevertheless, the ungual phalanx must have taken some of the weight, and *Schizotherium* was digitigrade rather than " metacarpograde ". *Grangeria* again seems to have had a digitigrade foot, though its ungual phalanges are unknown. Some degree of hyperextension at the metapodial-phalangeal joint is found in all perissodactyls, and the chalicotheres seem to have exaggerated this, first becoming digitigrade by modification of the distal end of the metapodial and probably receiving part of the weight on a pad in this region ; then the whole weight was received by the pad, thus permitting a higher degree of specialisation of the claws.

In *C. rusingense* and *C. grande*, if the basal phalanx is placed so that its most volar surface is horizontal in the transverse direction, the keels for articulation with the middle phalanx are approximately vertical, but the metatarsal is inclined so that its proximal end is medial to its distal end. This is probably the natural position, for the greater length of the third metatarsal is such as to bring its basal phalanx to the same level as that of the second digit. In *C. grande* the metatarsals increase in length from the second to the fourth. If they were held vertically, only the fourth digit would reach the ground, as Matthew (1929) pointed out.

There are objections to believing that *Chalicotherium* walked on the outside of its foot. The fourth metatarsal and metacarpal are no stouter than the others ; in fact in the manus the second metacarpal is the stoutest. In *Moropus* and *Ancylotherium*, again, the second metatarsal is shorter but stouter than the third, though unlike *Chalicotherium* the fourth is shorter than the third. Schaub concluded that in *Ancylotherium* the weight was taken by the radial digits (II and III). It seems highly probable therefore that in *Chalicotherium*, as well as in *Ancylotherium*, the second digit touched the ground. This must imply an inclination of the whole manus or pes towards the radial or tibial side. If the feet were orientated in a normal manner, with their dorsal sides facing forwards, the limbs would have to be spread out far laterally. It would be mechanically more efficient to bring the feet beneath the body by rotating them so that the toes pointed somewhat inwards, the shortest metapodial being then the most posterior, and it is suggested that this was the position in which *Chalicotherium* walked.

In maximum hyperextension the basal phalanx does not lie in line with the metapodial, but is turned so that its distal end is more lateral. The plane of rotation at the metapodial-phalangeal joint is inclined, so that the two bones come to lie in the same vertical plane only in maximum flexion. The two interphalangeal joints are not in the same plane ; if the joint between the basal and middle phalanges is considered as vertical, the joint between the middle and ungual phalanges is inclined so that its dorsal side is more lateral. The effect is that when the digit is extended it is curved towards the lateral side, but as it is flexed the claw is moved medially, till it lies parallel to and almost in line with the basal phalanx. Thus in the walking position the toes would point forwards, in spite of the medial rotation of the feet, while when the toe is flexed in order to use the claw, the metapodial, phalanges and claw are nearly in the same plane.

The dorsal position of the metacarpal facet on the basal phalanx of digit II of the manus in *Phyllotillon*, *Moropus* and probably in *Schizotherium*, may be related to the enlargement of the claw of that digit. If the claw rested on the ground in walking, the degree of hyperextension that would be required at the metapodial-phalangeal joint would be greater the larger the claw.

Schaub suggests that the elevation of the claws in *Ancylotherium* was an adaptation to avoid blunting when walking on hard ground. The lack of this adaptation in *Chalicotherium* would imply that the animal frequented ground too soft to cause serious damage to the claws. This accords with the view of Abel (1920) that *Chalicotherium* (" *Macrotherium* ") was an inhabitant of forest, where the ground would be covered with litter, while *Ancylotherium* (" *Chalicotherium* ") preferred more open country (savannah).

The shortness and stoutness of metacarpal II might be interpreted as an adaptation to clinging to tree-trunks in the manner postulated by Borissiak (1945) : the more

TABLE X.

Proportionate measurements (relative to length of M_2).

	C. rusingense		*C. grande*		*S. turgaicum*		*S. priscum*	
Length M_2 (mm.)	23·4–26·4 (mean 24·9)		36·5–38·5 (mean 37·5)		23·5		26	
	mm.	ratio	mm.	ratio	mm.	ratio	mm.	ratio
Scaphoid, width	57	2·3	49·5–56·5	1·4–1·5				
height	40	1·6	41·5–49	1·1–1·3				
thickness	40	1·6	35·5–44·5	1·0–1·2				
Metacarpals,								
Combined width II–IV			130	3·5			58	2·5
Combined width III–IV	58	2·3	92	2·4			36	1·5
III head, width	37·5	1·5	45–57	1·2–1·5			21	0·81
thickness	35·5	1·4	45–64·5	1·2–1·7			25	0·96
IV head, width	30	1·2	47–49	1·3	20	0·85	19	0·73
thickness	37	1·5	65–69	1·8	27	1·15	22	0·84
Length II			140–164	3·8–4·3			115	4·9
III			185–194	5·0–5·1			130	5·5
IV			187–220	5·1–5·7			126	5·4
Basal phalanges,								
Manus II, length	52·7–63	2·3–2·4	74–93	2·0–2·4				
width	32·8–39·5	1·4–1·5	51–60	1·4–1·6				
Manus III, length	57·7–67·5	2·5–2·6	76·5–97	2·1–2·5	29–49*	1·2–1·8	31·6–48*	1·2–1·8
width	30·2–35·6	1·3–1·4	52·5–66	1·4–1·7	16–29	0·68–1·2	18·5–29·6	0·71–1·14
Pes, length	37–42	1·6	56–64·5	1·5–1·7				
width	24·2–30·5	1·03–1·2	43–50	1·2–1·3				

Ungual phalanges,								
Manus, height . . .	37–49	1·6–1·9	67–73	1·8–1·9				
width . . .	19–26	0·81–0·98	31–36	0·85–0·93	12–13*	0·51–0·55	15·7–31*	0·60–1·2
Pes, height . . .	32–43	1·4–1·6	50·5–59·5	1·4–1·5	10–11	0·41–0·47	13–24	0·54–0·92
width . . .	20–30	0·85–1·1	26–31·5	0·71–0·82				
Astragalus, width . . .	67	2·7	100–111	2·7–2·9	43·5–47	1·8–2·0		
thickness . .	43·5	1·8	68–72·5	1·9	25–29	1·06–1·2		
medial height .	35·5	1·4	55·5–61	1·5–1·6	33	1·4		
Metatarsals,								
Combined width . .			125	3·3			57	2·4
II, length . . .	58–58·5	2·2–2·5	69–85·5	1·9–2·2	102–118	4·3–5·0	75	2·9
width head . .	26–27	1·02–1·1	37·5–40·5	1·03–1·05				
width distal . .	28–29	1·1–1·2	41–45	1·1–1·2				
III, length . . .	62·5–69	2·5–2·7	79	2·1	137	5·8	118	4·5
width head . .	23·5–25	0·95–1·0	34·5	0·92				
IV, length . . .			104	2·8			116	4·9

*In the species of *Schizotherium*, phalanges of the manus and pes have not been distinguished.

lateral digits would extend round the sides of the trunk and their greater length would be advantageous, but most of the pressure would be exerted by the second digit, which would be applied most perpendicularly to the surface of the trunk. In the pes, the short second digit might be associated with a straddling of the legs to give a firmer support, the claws presumably being dug into the ground.

Proportionate Sizes of Teeth and Feet.

In the absence of associated remains it is possible to make only a very rough estimate of the size of the feet in comparison with the teeth. The method used was to divide measurements of the bones of the feet by the mean length of M_2. Where more than one specimen of a bone is known, the largest specimen is compared with the largest specimen of M_2 and the smallest with the smallest specimen of M_2, obviously juvenile specimens being neglected. This was done also for specimens of *C. grande* from Sansan, for *Schizotherium turgaicum* and for *S. priscum*. (Table X.)

C. rusingense differs only slightly from *C. grande*. The greatest difference is its proportionately larger scaphoid, which suggests that the single specimen of this bone comes from an unusually large individual. Otherwise the differences are hardly significant : the head of the fourth metacarpal is smaller, the basal phalanx of the third digit of the manus is longer and narrower, the metatarsals are longer, and the ungual phalanges of the pes are broader.

Both species of *Chalicotherium* differ considerably from *Schizotherium*. The metacarpals are relatively broader, as is the manus as a whole. In *C. grande* metacarpals II and III are somewhat shorter than in *S. priscum*, but metacarpal IV is approximately of the same relative length. The pes of *C. grande* is much broader than that of *S. priscum*. In both species of *Chalicotherium* the astragalus is proportionately broader and thicker than in *S. turgaicum*, but of similar relative height, and the metatarsals are much shorter than in *S. priscum*. The phalanges of the manus are proportionately much larger in all dimensions in *Chalicotherium* than in *Schizotherium*.

RELATIONSHIPS.

In the foregoing description *C. rusingense* has been compared mainly with *C. grande*, the best-known member of the Chalicotheriinae, and with species of *Schizotherium* (*S. priscum* and *S. turgaicum*), the most primitive genus of Schizotheriinae. It shows resemblances to both these forms, but the resemblances to *C. grande* are of greater taxonomic value, whereas those to *Schizotherium* are primitive characters inherited from the common ancestor of *Chalicotherium* and *Schizotherium*, perhaps in the Lower Oligocene.

C. rusingense is close to *C. grande* in (1) the upper molar pattern, (2) the loss of the hypoconulid of M_3, (3) the reduction of the scaphoid-magnum contact, (4) characters of the head of metacarpals III and IV, (5) the broad, short metatarsals, those of digits II and III being equal in width, (6) the astragalus, which is reduced in height, and also reduced in thickness in the fibular half, (7) the greater size of the phalanges of the manus as compared with those of the pes, (8) the form of the articulating facets on the phalanges, associated with the development of a metacarpograde stance, and (9) the ungual phalanges, which are narrower and less hoof-like than in *Schizotherium.*

At the same time *C. rusingense* is more primitive than *C. grande* in several respects in which it approaches *Schizotherium* : (1) the smaller size, (2) some features of the upper molar pattern—the protocone is frequently connected to the protoconule by a ridge, the ridge on the buccal slope of the paracone is sharper, and the accessory rib in the postfossette is frequently present, (3) the presence in most specimens of a metastylid on the lower molars, (4) the smaller degree of reduction of the premolars, (5) the greater elongation of the anterior part of the jaws, (6) the astragalus, in which the trochlea is higher and the navicular facet is less tilted towards the tibial side. (7) the less thickened metatarsals, (8) the absence of a distinct cuboid facet on metatarsal III, and the presence of two separate facets for articulation with metatarsal IV, (9) the longer basal phalanges, especially on digit III of the manus, and (10) the better development of intermediate volar tubercles on the basal phalanges.

C. pilgrimi agrees with *C. rusingense* in size, in the presence of a metastylid on the lower molars, and in the characters of metatarsal II, but the upper molars of *C. pilgrimi* are more primitive in that the paracone and metacone have not receded so far from the buccal edge of the tooth. *C. wetzleri* agrees with *C. rusingense* in the metastylid, and perhaps in the elongation of the snout and characters of the phalanges. *C. salinum,* though much nearer to *C. grande,* shows some primitive features in the sharpness of the buccal paracone crest and the retention of the protocone-protoconule crest.

C. rusingense must therefore be regarded as a persistently primitive form not closely related to other species of the genus. Its interest lies mainly in the light it throws on the evolutionary changes involved in the derivation of the Chalicotheriinae from a form close to *Schizotherium.*

Subfamily Schizotheriinae

ANCYLOTHERIUM AND RELATED GENERA

Ancylotherium pentelicum (Gaudry & Lartet 1856) is a characteristic member of the Pontian fauna of Pikermi, Samos and other localities in S.E. Europe, extending to Maragha in Iran (de Mecquenem 1924). Thenius (1953) pointed out the resemblances between this species and *Metaschizotherium fraasi* von Koenigswald (1932), from the Upper Miocene of Germany and France, and proposed to include the genus *Metaschizotherium* in *Ancylotherium.* Viret (1949) had previously considered *M. fraasi* to be almost identical with *Phyllotillon naricus* (Pilgrim 1908, 1910) from the Lower Miocene of Baluchistan. It is also necessary to consider *Phyllotillon betpakdalensis* (Flerov 1938), from the Upper Oligocene of Kazakhstan, which has been described in great detail by Borissiak (1946).

The upper molars of *A. pentelicum* (Thenius 1953, Wagner 1857), *M. fraasi* (Fraas 1870, Depéret 1892, von Koenigswald 1932), *P. naricus* (Pilgrim 1912, Forster Cooper 1920) and *P. betpakdalensis* (Borissiak 1946) are so much alike that the relationship of the species cannot be doubted. The molars of *P. naricus* show a considerable range of size (length of M^3 40–48 mm.; length of M^2 40–49 mm.): the specimens identified as milk-molars by Pilgrim (1912, pl. 12, fig. 3) are small examples of permanent molars. *M. fraasi* falls within the lower part of the size range of *P. naricus*. It is doubtful whether *M. bavaricum* von Koenigswald (1932) is specifically distinct from *M. fraasi*. *P. betpakdalensis* is very variable and reaches a larger size (length of M^3 42–60 mm.). *A. pentelicum* equals or slightly exceeds the largest specimens of *P. betpakdalensis*. According to Thenius (1953) *A. pentelicum* differs from *M. fraasi* in the more elevated ectoloph and the weaker cingulum, but the differences do not appear to be great. *P. betpakdalensis* stands apart in (1) the stronger development of the buccal cingulum, (2) the straighter protoloph, which runs almost directly to the tip of the protocone, instead of bending sharply to pass up the anterior slope of the protocone, and (3) the strong development of the cingulum round the base of the hypocone in some specimens of M^3, with the formation of additional cingular cusps in that region (Borissiak regarded the hypocone as a metaconule, and the cingular cusps as representing the hypocone).

There are some differences in the upper premolars. In *P. naricus* the deuterocone on P^3 and P^4 is conical, with a convex buccal slope; it is connected to the ectoloph by a protoloph and a metaloph. In *P. betpakdalensis* the buccal slope of the deuterocone forms a more definite ridge. In *A. pentelicum* the deuterocone is crescentic, apparently with a flattened buccal slope. A specimen of P^4 referred to *M. bavaricum* by von Koenigswald (1932) and a similar tooth figured by Roger (1885) are partly molarized: a small crest branches off from the metaloph to join the posterior cingulum.

The lower molars of *P. naricus*, *P. betpakdalensis* and *M. fraasi* are very similar in structure. The only lower molar of *A. pentelicum* that has been figured is M_1 in a juvenile mandible (Dietrich 1928). A strongly developed metastylid is characteristic of the group.

Specimens and casts show that in *P. naricus* and *P. betpakdalensis* the infraorbital foramen is situated above M^2, as in *Moropus*, whereas in *Chalicotherium* and in *Schizotherium priscum* it is farther forward, above M^1. The mandibles of *P. naricus*, *P. betpakdalensis* and *A. pentelicum* (Falconer 1868) are distinguished from those of *Chalicotherium* in the short symphysis, which does not extend back as far as P_2. According to Falconer (1868), and Major (1894), *A. pentelicum* lacks the lower canine and incisors, but a specimen of *P. naricus* shows traces of alveoli at the anterior end of the mandible. A juvenile mandible from St. Gérand-le-Puy, described by Filhol (1879) as *Chalicotherium modicum*, and now in Paris, has a short symphysis like *P. naricus* and may be referred to the genus *Phyllotillon*. At the anterior end it shows a large alveolus, probably for a lower canine.

The lower end of the humerus of *P. betpakdalensis* differs from *A. pentelicum* and from *Moropus* in the shape of the articulatory surfaces, but resembles *Schizotherium turgaicum*. The radius and ulna are more slender than in *A. pentelicum*; the radius is less flattened at its distal end, and fusion with the ulna is less complete.

Except for a lunate of *M. fraasi* described by Rinnert (1956), the carpals are known only in *P. betpakdalensis* (Borissiak 1946) and *A. pentelicum* (Schaub 1943).

Those of *P. betpakdalensis* differ from *A. pentelicum* mainly in a primitive direction: for example, the scaphoid is comparatively deep, with a well developed distal process as in *Moropus*; the lunate has a prominent volar process; the trapezoid and unciform are relatively narrow and deep, and the carpus as a whole is deeper, with more oblique articulatory facets. The lunate of *M. fraasi* resembles that of *A. pentelicum.*

P. betpakdalensis has a fifth digit on the manus, lost in *A. pentelicum.* Metacarpals II–IV are less flattened than in *A. pentelicum,* and do not show the dorsal concavity characteristic of that species.

The astragalus of *P. betpakdalensis* is higher than in *A. pentelicum,* and differs in the possession of a cuboid facet. That of *M. fraasi* (von Koenigswald 1932, Thenius 1953, Rinnert 1956) resembles *A. pentelicum.* In all three species the ectal facet is deeply concave, in contrast with the much shallower facet of *Chalicotherium.* The calcaneum is similar in the three species. In *P. betpakdalensis* the cuboid, navicular and ectocuneiform are much less flattened than in *A. pentelicum*; the cuboid of *M. fraasi* (Rinnert 1956) resembles that of *A. pentelicum.*

The metatarsals of *P. betpakdalensis* are much more slender than those of *A. pentelicum.* Phalanges of all four species are known: some of the phalanges described by Forster Cooper (1920) from the Bugti Beds are almost certainly those of *P. naricus.* Except in *P. betpakdalensis* the basal and middle phalanges of digit II normally unite. In *A. pentelicum* the basal phalanges are more flattened at the distal end than in the other species, so that the surface for articulation with the middle phalanx makes a smaller angle with the long axis of the bone. The known basal phalanges of *P. betpakdalensis* are much smaller than those of *A. pentelicum* (length 55–70 mm. compared with 91–114 mm.), although there is less discrepancy in the teeth; it is possible therefore that the toes of *P. betpakdalensis* were proportionately smaller, as in *Schizotherium.*

This comparison shows that *P. betpakdalensis* stands apart from the other species. In several respects it is much more primitive than *A. pentelicum,* as would be expected from its earlier age, but it shows some specializations, such as the cuboid-astragalus contact and the large size, which exclude it from the ancestry of the later species. I therefore propose to make it the type species of a new genus.

Genus ***BORISSIAKIA*** nov.

Diagnosis. Schizotheriine chalicotheres of large size, in which the protoloph runs directly to the tip of the protocone, the scaphoid and lunate resemble those of *Moropus,* there are four digits on the manus, and the astragalus articulates with the cuboid.

Type and only known species, *Moropus betpakdalensis* Flerov (1938).

Genus ***PHYLLOTILLON*** Pilgrim, 1910

Phyllotillon naricus and *Metaschizotherium fraasi* are very close, and may be conspecific as Viret (1949) suggested. *Metaschizotherium* therefore becomes a synonym of *Phyllotillon.* This genus first appears as a small unnamed species in the

Upper Oligocene of St. Gérand-le-Puy (Filhol 1879), and thus coexisted with *Borissiakia betpakdalensis*. *Phyllotillon* is probably the ancestor of *Ancylotherium*, from which it may be distinguished by primitive characters : (1) teeth present at the anterior end of the mandible (in *Ancylotherium* lower incisors and canine have disappeared) ; (2) distal ends of basal phalanges of digits III and IV less flattened. Unfortunately the skeleton is poorly known.

Genus ***ANCYLOTHERIUM*** Gaudry, 1862

Ancylotherium hennigi (Dietrich)

Text-figs. 21A–D, 22A–D, 23A–D, 24, 25A, B, 26A, B.

1923 Chalicothere, Andrews, p. 696.
1926 Chalicotheridae, gen. et sp. indet., Hopwood, p. 19, text-fig. 1.
1942 *Metaschizotherium hennigi* Dietrich, p. 105, pl. 4, figs. 33, 37, pl. 12, figs. 78–80, 83.
1943 *Metaschizotherium hennigi* Dietrich ; Schaub, pp. 19, 25.
1950 *Metaschizotherium transvaalensis* George, p. 241, text-figs. 1, 2.
1951 *Metaschizotherium hennigi* Dietrich ; Hopwood, p. 21.
1953 *Ancylotherium hennigi* (Dietrich) Thenius, p. 103.

The occurrence of this chalicothere in Bed I at Olduvai, Tanganyika, has been reported by Hopwood (1951). The material consists of eight specimens, all from the left manus, and all collected on the same day from site THC, layer I 5. It is therefore likely to have been derived from a single individual. The specimens, which are preserved in the British Museum (Natural History), may be listed as follows :

M18785, scaphoid.
M18783, lunate.
M18784, cuneiform.
M18786, second metacarpal.
M18782, third metacarpal.
M18780, proximal phalanx.
M18781, two middle phalanges.

The scaphoid (Text-fig. 21 A–D) shows much resemblance to that of *A. pentelicum*. In proximal view it is trapezoidal rather than triangular in shape, owing to its broader volar process and flatter dorsal surface. The width (64.5 mm.) and length (75.5 mm.) are somewhat less than in the specimen measured by Schaub (1943), but greater than in a cast seen in the Paris Museum. The height (48 mm.) is proportionately greater than in *A. pentelicum*. The proximal surface is mainly occupied, as in *A. pentelicum*, by the articulation for the radius, which is nearly flat, but slightly concave in the dorsovolar direction, extending down on to the dorsal surface near the ulnar side. The articulation for the trapezoid on the distal surface is rectangular, rather than ovoid as in *A. pentelicum*. It is concave in the middle, but towards the dorsal and volar sides it is crossed by two transverse convexities, that on the volar side being the sharper of the two. The articulating surface is continuous with that for the magnum, the line of separation being marked by a blunt dorsovolar ridge which rises to a cusp near each end. The magnum facet is broader near its volar end and extends as a tongue (rather broader than in *A. pentelicum*) to near the dorsal side. On the ulnar side there are two facets for the lunate, more widely separated than in

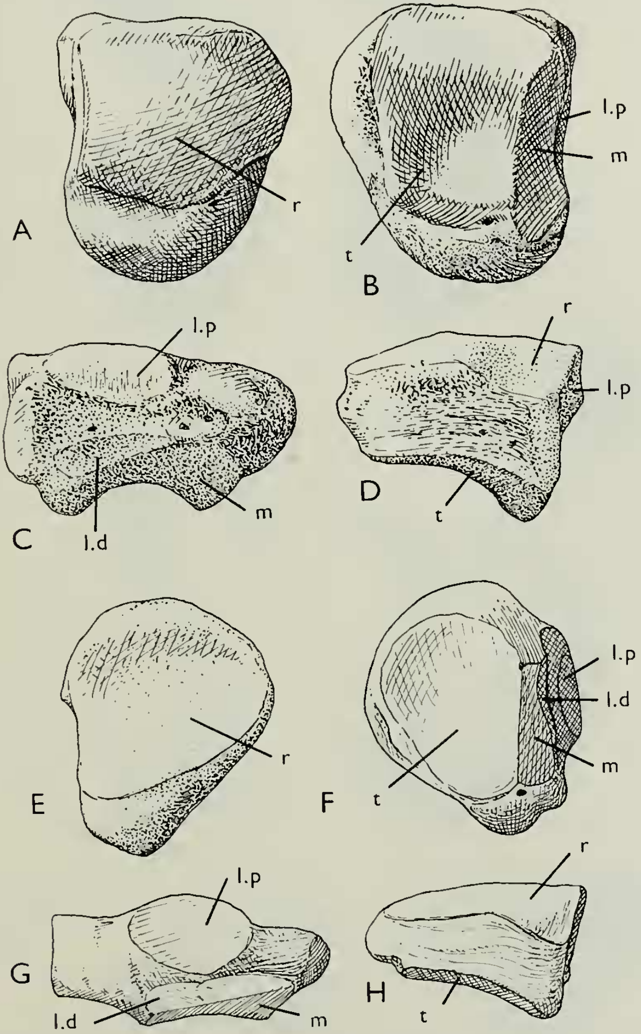

FIG. 21. Left scaphoids of *Ancylotherium*. A–D, *A. hennigi*, BMNH. M18785. A, proximal view ; B, distal view ; C, ulnar view ; D, dorsal view. E–H, *A. pentelicum*, Paris specimen, corresponding views. All × ½.
Key to facets : *l.d. l.p.*, lunate (distal and proximal) ; *m*, magnum ; *r*, radius ; *t*, trapezoid.

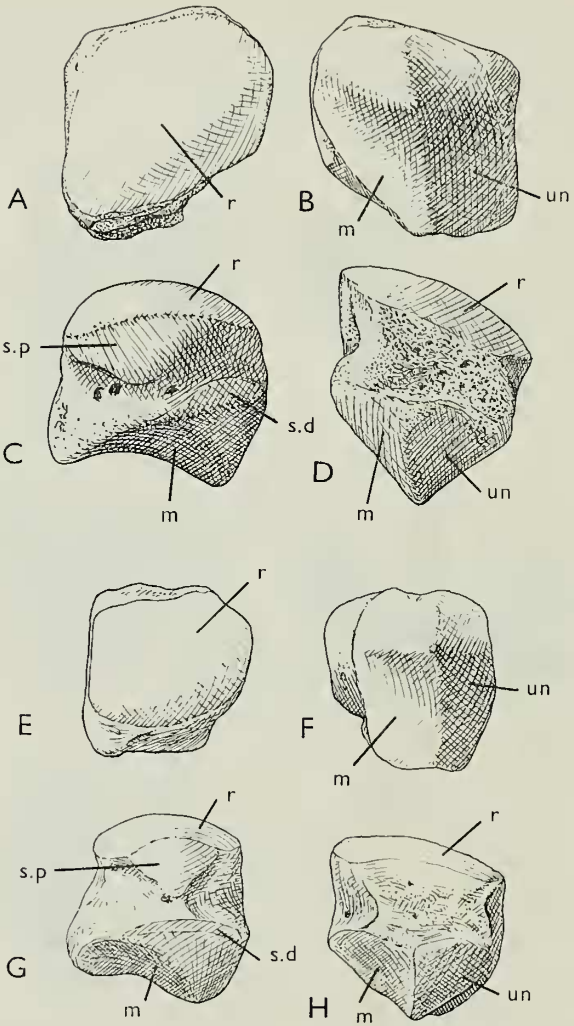

Fig. 22. Left lunates of *Ancylotherium*. A–D, *A. hennigi*, BMNH. M18783. A, proximal view ; B, distal view ; C, radial view ; D, dorsal view. E–H, *A. pentelicum*, Paris specimen, corresponding views. All × ½.
Key to facets : *m*, magnum ; *r*, radius ; *s.d*, *s.p*, scaphoid (distal and proximal) ; *un* unciform.

A. pentelicum ; the distal one is slightly concave, and separated from the magnum facet only by a blunt ridge ; the proximal lunate facet is flat, and makes an angle of about 70° with the radius facet.

The lunate (Text-fig. 22 A–D) (width 64 mm., length 61 mm., height 58 mm.) is somewhat smaller than Schaub's specimen, and larger than a cast measured in Paris.

In comparison with the Paris cast it appears in proximal view to be more drawn out in an oblique direction from radiodorsal to ulnovolar. The proximal surface is completely occupied by the articulating surface for the radius, more definitely rhomboidal than in *A. pentelicum*, but as in that species convex in the dorsovolar direction and to a lesser degree also in the transverse direction. The radial surface bears as in *A. pentelicum* a proximal facet for the scaphoid, flat and triangular, and

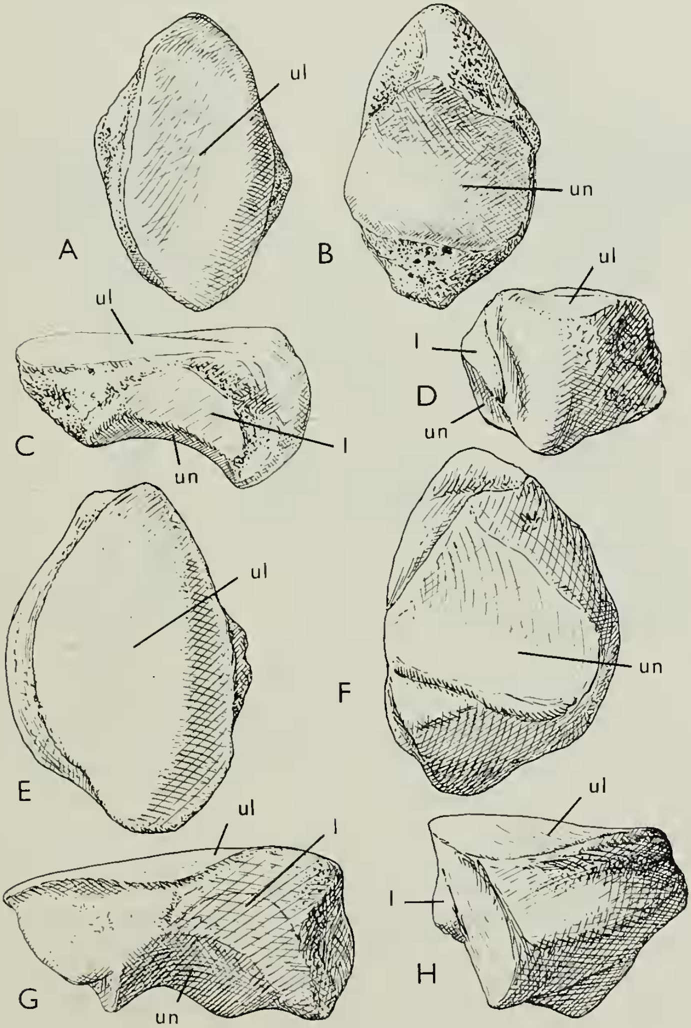

FIG. 23. Cuneiforms of *Ancylotherium*. A–D, *A. hennigi*, BMNH. M18784, from left manus. A, proximal view; B, distal view; C, radial view; D, dorsal view. E–H, *A. pentelicum*, BMNH. M11346, from right manus (reversed), corresponding views. All × $\frac{1}{2}$.
Key to facets: *l*, lunate; *ul*, ulna; *un*, unciform.

divided from the smaller, elongated, convex distal scaphoid facet by a groove, into which open some nutritive foramina. The distal surface is divided by a rounded ridge which connects a dorsal to a volar cusp, and separates the articulatory surfaces for the magnum and the unciform. Each of these surfaces is convex dorsally and concave in its central and volar parts. In comparison with *A. pentelicum* the distal surface is triangular rather than quadrate, as the volar process is small and situated more towards the ulnar side of the bone. On the ulnar side the articulation for the unciform passes insensibly into that for the cuneiform, which is confined to the distal part of the ulnar side.

The cuneiform (Text-fig. 23 A–D) (width 53.5 mm., length 82 mm., height 43.5 mm.) is slightly smaller than the British Museum specimen of *A. pentelicum* (M11346), which it closely resembles. It is a flattened bone, ovoid in proximal view, with the greatest diameter from radiodorsal to ulnovolar. Most of the proximal surface is occupied by the articulating facet for the ulna, concave in a dorsovolar direction. Near the volar edge this facet adjoins that for the pisiform, the separation being merely by a gentle convexity. On the distal surface of the cuneiform is the saddle-shaped facet for the unciform, concave in a dorsovolar direction and slightly convex transversely. This facet occupies rather more of the central portion of the distal surface than in *A. pentelicum*. Radially it adjoins the facet for the lunate. The height of the cuneiform is greatest near its dorsal side.

The second metacarpal (Text-fig. 24) has suffered some surface damage at its proximal end, and the distal end is lacking. As preserved, the distal surface possesses radially arranged ridges on the surface of the spongiosa which indicate that the epiphysis was still separate. The thin compacta, with numerous vascular canals, supports the view that the specimen was a juvenile. The metacarpal is slightly smaller than the corresponding bone of *A. pentelicum* in the British Museum (M4426) (the greatest length as preserved is 165 mm.). In proximal view the head of the bone appears more compressed laterally than in *A. pentelicum*. There is a prominent dorso-ulnar process and a small radial process. The centre of the proximal surface is occupied by the facet for the trapezoid, flattened and slightly saddle-shaped, and not so definitely concave as in *A. pentelicum*. On its ulnar side is a flat facet for the magnum, narrower than in *A. pentelicum*. On the ulnar side of the bone, adjoining the magnum facet, is the overhung facet for metacarpal III, forming the proximal border of a pit. Schaub (1943) identified in *A. pentelicum* a smooth area immediately to the volar side of the trapezoid facet as a surface which contacted the scaphoid in extreme flexion of the carpus. An apparently corresponding area can be recognised in *A. hennigi*, but it is less distinct from the trapezoid facet. Another smooth area on the volar surface of the radial process may have had the same function. The shaft of the metacarpal is straight and nearly as thick as wide in the middle of its length ; it does not show the dorsovolar flattening of *A. pentelicum*. The radial surface is smoothly convex transversely, very slightly concave longitudinally. The dorsal surface is marked by a longitudinal shallow groove which arises proximally about 5 cm. below the dorsal apophysis and fades out distally. It corresponds to a much broader and deeper groove in *A. pentelicum*, where the dorsal and ulnar surfaces are divided by a prominent crest ; this crest is very poorly developed in *A. hennigi*. In both species the ulnar surface is scarred near its proximal end for ligamentary attachment, and the proximal part of the volar surface is irregularly pitted and pierced by numerous foramina. Immediately distal to the pitted area the volar surface is roughened for ligamentary attachment. In *A. hennigi* the volar surface is more convex transversely than in *A. pentelicum*.

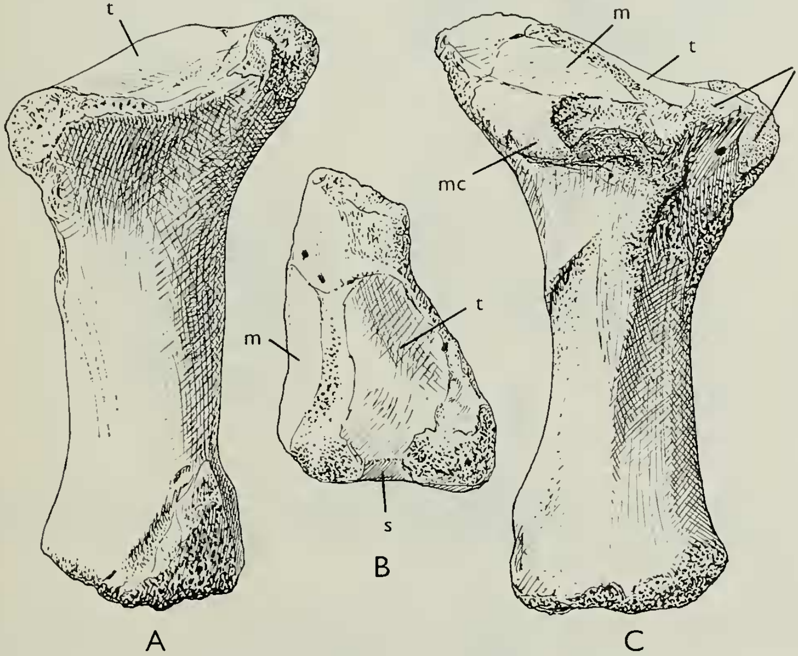

FIG. 24. Left second metacarpal of *Ancylotherium hennigi*, BMNH. M18786, A, dorso-radial view ; B, proximal view ; B, ulnovolar view. All × $\frac{1}{2}$.
Key : *m*, magnum facet ; *mc*, facet for metacarpal III ; *s*, possible contacts with scaphoid ; *t*, trapezoid facet.

Both ends of the third metacarpal have broken off. The shaft is broader and flatter than that of metacarpal II, but in comparison with *A. pentelicum* the ulnar side of the bone is much thicker, the dorsal longitudinal groove is less marked, and the ridge separating the dorsal and ulnar surfaces is less developed. As in *A. pentelicum* the dorsal surface is concave in a longitudinal direction. On the volar side there is a rather deep longitudinal groove, more marked than in *A. pentelicum*. The ulnar surface is extensively roughened, especially proximally. The proximal part of the radial surface shows a slight longitudinal groove. The proximal end of a third metacarpal of *A. hennigi* has been described by Dietrich (1942), but his description is not sufficiently detailed to permit comparison with *A. pentelicum*.

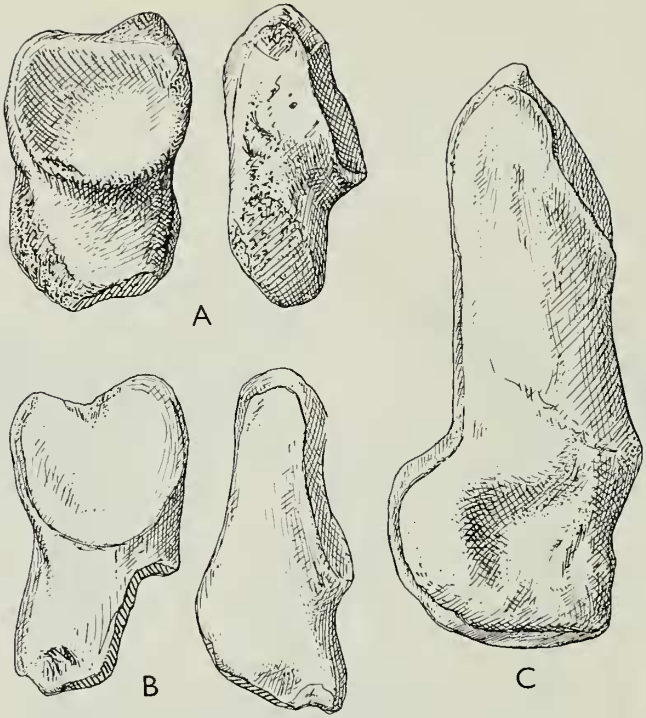

FIG. 25. A, *Ancylotherium hennigi*, basal phalanx, BMNH. M18780, dorsal and side views. B, BMNH. M12673, from Kaiso, dorsal and side views. C, *A. pentelicum*, co-ossified basal and middle phalanges, BMNH. M9044, side view. All × ½.

The basal phalanx (Text-fig. 25A, B) shows most resemblance to one of Major's specimens of *A. pentelicum*, referred by Schaub (1943, fig. 22) to digit IV of the manus. However, it is shorter (length 81 mm., against 105 mm. in Major's specimen) and less broadened at the proximal end (width 52 mm., against 65 mm.). The Pikermi specimen in Paris differs from both of these in being fused with the middle phalanx. The distal half of the phalanx is much flattened, the dorsovolar diameter of the shaft being only about 60% of the transverse diameter. The articulatory surface for the middle phalanx is flattened and displaced to the volar side of the bone. The metacarpal articulation faces somewhat more dorsally than in the phalanx of *A. hennigi* described by Dietrich (1942) and referred by Schaub (1943) to digit IV, but both specimens agree in the presence of a step in the dorsal surface immediately distal to the articulation ; this step occurs also in Major's specimen of *A. pentelicum*. Dietrich's specimen is a little larger (length 92 mm., proximal breadth 59 mm.), but more narrowed at the distal end.

The phalanx from the Pleistocene of Kaiso, Uganda (Andrews 1923, Hopwood 1926) is similar in size to the Olduvai specimen, but differs in a number of respects. The metacarpal articulation lies nearly in the plane of the dorsal surface, and is proportionately longer and narrower ; the proximal end of the bone is flatter, and the distal end much deeper. The distal end is broken, and it seems possible that its depth is due to fusion with the middle phalanx. This specimen is referred to digit II of the manus, probably of *A. hennigi*.

The two middle phalanges (Text-fig. 26A, B) resemble *A. pentelicum* in the relatively flat proximal articulation, with a rather weak median ridge, and in the shallow trochlear groove at the distal end. One specimen fits the basal phalanx, and may therefore be referred to digit IV. It differs from the second specimen in being shorter, in having a more vertical proximal articulation (the proximal volar process being less prominent) and a shallower trochlear groove. The specimen described by Dietrich (1942) resembles the middle phalanges from Olduvai, but it is much smaller, and was probably correctly referred by Dietrich to the pes.

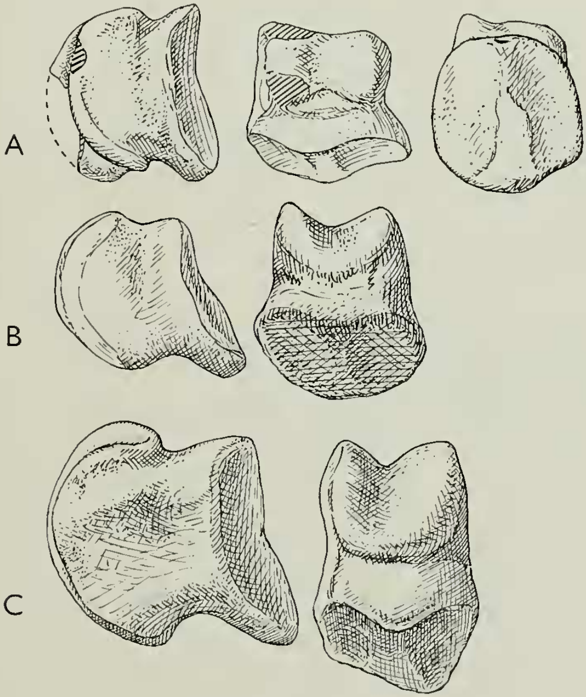

FIG. 26. Middle phalanges of *Ancylotherium*. A, B, *A. hennigi*, BMNH. M18781. C, *A. pentelicum*, BMNH. M9042. All × ½.

The Olduvai chalicothere resembles *Ancylotherium pentelicum* in numerous details of the bones of the manus, and it is therefore placed in the genus *Ancylotherium* rather than *Phyllotillon* (=*Metaschizotherium*). The resemblance of *Metaschizotherium hennigi* to *A. pentelicum* was previously noted by Schaub (1943), and Thenius (1953) transferred *M. hennigi* to *Ancylotherium*. The Olduvai material is almost certainly to be identified as *A. hennigi*, but direct comparison is possible only to a very limited extent owing to the fragmentary nature of the material. This also applies to *Metaschizotherium transvaalensis* George (1950), based upon an ungual phalanx and some teeth from Makapansgat. To judge from the published figures, upper molars from Makapansgat and the Serengeti are very similar, in spite of a difference in length/breadth index, and specific distinction seems hardly justified on present knowledge.

A. hennigi differs from *A. pentelicum* notably in that the metacarpals are less flattened and hollowed out dorsally, and the scaphoid is deeper. This suggests that *A. hennigi* was less specialised than the Pontian species and not directly derived from it.

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